VOLUME 134 PART 4 SEPTEMBER 1960

PROCEEDINGS

OF

THE ZOOLOGICAL SOCIETY OF LONDON

LONDON
PUBLISHED BY THE SOCIETY
SOLD AT ITS HOUSE IN REGENT'S PARK, LONDON, N.W.

Price Thirty Shillings

THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.

Clerk of Publications . . . G. B. STRATTON, M.B.E.

The **Proceedings,** founded in 1830, are published in royal octavo form and constitute the principal organ of the Society for the publication of original works in zoology, and for notices of the business transacted at the Scientific Meetings of the Society.

Two volumes are published annually ; each volume containing four numbers. Price per volume £6 ; separate numbers £1 10*s.* 0*d.* each.

The **Transactions,** founded in 1833, are published in quarto form and contain those papers and monographs which by reason of the size of the illustrations, are better adapted for publication in that format. The " Transactions " are published at irregular intervals at prices varying in accordance with the cost of production.

OTHER PUBLICATIONS OF THE SOCIETY

The Zoological Record, founded in 1864, is issued annually with the object of providing a complete list of references to publications in zoology in all its branches for each year of issue. The Society is unable to supply *complete sets* of the " Record " as several volumes are now out of print. The following volumes are available :—

Vols. 65–71 (1928–1934) at £5 each.
Vols. 85–91 (1948–1954) at £6 each.
Vols. 92-94 (1955-1957) at £8 each.

REPRINT EDITION. Vols. 1–25 (1864–1889). Obtainable only from Messrs. Butterworths, 88 Kingsway, London, W.C.2.

Complete set, cloth, £208.2s.0d.; paper covers, £199.12s.6d.
Selected volumes, paper bound, only, £8.18s.6d. per vol.
The part " Insecta " sold separately, paper bound, price £5 per volume, £125 per set of 25 volumes.

Nomenclator Zoologicus. The five volumes contain the names of all the genera and subgenera in zoology from the 10th Edition of Linnaeus 1758 to the end of 1945, with a bibliographical reference to the original description of each. Price 17½ guineas, postage extra. Price of the separate volumes : Vols 1–4 (1758–1935) ; Vol. 5 (1936-1945) 3½ guineas each, postage extra.

THE INNER EAR OF SOME MEMBERS OF THE PIPIDAE (AMPHIBIA).

BY

NELLIE F. PATERSON

Department of Zoology, University of Cape Town

[Accepted 10th November 1959]

(With 14 figures in the text)

The aquatic habit of members of the Pipidae seems to have resulted in the retention of a number of neotenic features, and these are evident in the inner ear as well as in other systems of organs.

From a comparative study of the morphological details of the inner ear of adults of *Hemipipa carvalhoi*, *Hymenochirus curtipes* and *Xenopus laevis*, juvenile *Pipa pipa* and larval stages of *Hemipipa*, *Xenopus* and *Rana fascigula*, it appears that the arrangement in *Hemipipa* is the least specialized, while the inner ear of *Xenopus* closely resembles that of amphibious Anura.

Attention is drawn to Witschi's conclusions (1947–1956) that in larval forms of *Rana* and *Xenopus* the lungs act as sound receptors, associated with which is the temporary development of certain auxiliary bronchial structures. In the present observations these structures are interpreted otherwise, and no definite conclusions are reached as to their participation in the auditory mechanism.

Variations in the inner ear of the four species of Pipidae studied appear to strengthen opinions regarding the somewhat unsatisfactory classification of the family. *Hemipipa* and *Pipa* fall naturally into the subfamily Pipinae, but the marked differences between *Hymenochirus* and *Xenopus*, not only in regard to the inner ear, but also in other anatomical features, suggest that these two genera should be relegated to separate subfamilies.

CONTENTS

	Page
Introduction	509
Comparative account of the pipid inner ear	516
Innervation of the labyrinth	521
Endolymphatic system	525
Perilymphatic system	528
Conclusions	535
Acknowledgments	541
Summary	542
Addendum	542
References	543
Key to the lettering of figures	545

INTRODUCTION

For many years the ear of various species of fishes and frogs has proved to be a convenient subject of experimental investigation and, consequently, there is a considerable volume of published work dealing with the morphology and probable physiology of the component parts of both the inner and middle ear in members of these two classes.

The underlying structural uniformity of the ear in all classes of vertebrates and the gradual increase in complexity from the Agnatha to the Mammalia have been circumstantially described by de Burlet (1934), while valuable information relating to the morphology and physiology of the parts of the

THE PROCEEDINGS OF THE ZOOLOGICAL SOCIETY OF LONDON

THE TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

Editor . . . . . L. HARRISON MATTHEWS, F.R.S.

Clerk of Publications . . . G. B. STRATTON, M.B.E.

The **Proceedings,** founded in 1830, are published in royal octavo form and constitute the principal organ of the Society for the publication of original works in zoology, and for notices of the business transacted at the Scientific Meetings of the Society.

Two volumes are published annually ; each volume containing four numbers. Price per volume £6 ; separate numbers £1 10*s.* 0*d.* each.

The **Transactions,** founded in 1833, are published in quarto form and contain those papers and monographs which by reason of the size of the illustrations, are better adapted for publication in that format. The " Transactions " are published at irregular intervals at prices varying in accordance with the cost of production.

OTHER PUBLICATIONS OF THE SOCIETY

The Zoological Record, founded in 1864, is issued annually with the object of providing a complete list of references to publications in zoology in all its branches for each year of issue. The Society is unable to supply *complete sets* of the " Record " as several volumes are now out of print. The following volumes are available :—

Vols. 65–71 (1928–1934) at £5 each.
Vols. 85–91 (1948–1954) at £6 each.
Vols. 92-94 (1955-1957) at £8 each.

REPRINT EDITION. Vols. 1–25 (1864–1889). Obtainable only from Messrs. Butterworths, 88 Kingsway, London, W.C.2.

Complete set, cloth, £208.2s.0d.; paper covers, £199.12s.6d.
Selected volumes, paper bound, only, £8.18s.6d. per vol.
The part " Insecta " sold separately, paper bound, price £5 per volume, £125 per set of 25 volumes.

Nomenclator Zoologicus. The five volumes contain the names of all the genera and subgenera in zoology from the 10th Edition of Linnaeus 1758 to the end of 1945, with a bibliographical reference to the original description of each. Price 17½ guineas, postage extra. Price of the separate volumes : Vols 1–4 (1758–1935) ; Vol. 5 (1936–1945) 3½ guineas each, postage extra.

THE INNER EAR OF SOME MEMBERS OF THE PIPIDAE (AMPHIBIA).

BY

NELLIE F. PATERSON

Department of Zoology, University of Cape Town

[Accepted 10th November 1959]

(With 14 figures in the text)

The aquatic habit of members of the Pipidae seems to have resulted in the retention of a number of neotenic features, and these are evident in the inner ear as well as in other systems of organs.

From a comparative study of the morphological details of the inner ear of adults of *Hemipipa carvalhoi*, *Hymenochirus curtipes* and *Xenopus laevis*, juvenile *Pipa pipa* and larval stages of *Hemipipa*, *Xenopus* and *Rana fuscigula*, it appears that the arrangement in *Hemipipa* is the least specialized, while the inner ear of *Xenopus* closely resembles that of amphibious Anura.

Attention is drawn to Witschi's conclusions (1947–1956) that in larval forms of *Rana* and *Xenopus* the lungs act as sound receptors, associated with which is the temporary development of certain auxiliary bronchial structures. In the present observations these structures are interpreted otherwise, and no definite conclusions are reached as to their participation in the auditory mechanism.

Variations in the inner ear of the four species of Pipidae studied appear to strengthen opinions regarding the somewhat unsatisfactory classification of the family. *Hemipipa* and *Pipa* fall naturally into the subfamily Pipinae, but the marked differences between *Hymenochirus* and *Xenopus*, not only in regard to the inner ear, but also in other anatomical features, suggest that these two genera should be relegated to separate subfamilies.

CONTENTS

	Page
Introduction	509
Comparative account of the pipid inner ear	516
Innervation of the labyrinth	521
Endolymphatic system	525
Perilymphatic system	528
Conclusions	535
Acknowledgments	541
Summary	542
Addendum	542
References	543
Key to the lettering of figures	545

INTRODUCTION

For many years the ear of various species of fishes and frogs has proved to be a convenient subject of experimental investigation and, consequently, there is a considerable volume of published work dealing with the morphology and probable physiology of the component parts of both the inner and middle ear in members of these two classes.

The underlying structural uniformity of the ear in all classes of vertebrates and the gradual increase in complexity from the Agnatha to the Mammalia have been circumstantially described by de Burlet (1934), while valuable information relating to the morphology and physiology of the parts of the

amphibian ear in particular has accrued from the observations of scores of workers, including Gaupp (1896–1904), Harrison (1902), Gruenberg (1907), Reed (1920), Greene & Laurens (1923), McNally & Tait (1925–26) and MacNaughton & McNally (1946). It is also evident from the reviews by von Frisch (1936) and Lowenstein (1936) and the findings of Lowenstein & Roberts (1948, 1950, 1951) that earlier speculation concerning the physiology of the parts of the vertebrate ear has been placed on a sounder basis largely as the outcome of patient experimental work performed on Pisces and Amphibia.

While the results of some of the experiments may have been somewhat inconclusive or even contradictory, reliable proof seems to be emerging as to the precise function of the individual parts of the ear. There is thus a general acceptance of the principles of the mechanisms concerned in sound conduction in the different classes of vertebrates and also of some of the theories of the evolution of the parts of the middle ear, leading up to the arrangement of the auditory ossicles in the Mammalia.

In this connexion the Amphibia are of interest for, consequent upon their transition from aquatic to terrestrial life, marked morphological modifications become apparent in their sound transmitting apparatus. This seems to be better illustrated in the Urodela than in the Anura, for it has long been estabished that there is a radical difference between the method of sound reception in larval and mature aquatic urodeles and that employed by their terrestrial congeners. In Anura, however, although the adult ear has been subjected to exhaustive research and much is known about its physiology, the circumstances in premetamorphic stages are imperfectly understood.

Interest in the problems involved seems to have been revived recently, and the opinions expressed by some of the workers serve to focus attention on certain of the more controversial points. In his review of sound transmission throughout the vertebrates, Tumarkin (1948 a) recognizes six main types of auditory conducting mechanisms and shows that the Urodela employ either the vestibulo-squamosal or the vestibulo-scapular method, according to their particular habits and habitats, while in the Anura the mechanism is vestibulo-scapular in a few but vestibulo-tympanic in the majority. His articles (1948 a, b) are also of interest in that he expresses strong disapproval of the ' orthodox ' theory of the evolution of the auditory ossicles. On the basis of the physiology of the parts he suggests, among other things, that the early Amphibia did not possess a tympanic membrane and also concludes that the anuran columella auris is not homologous with that of the Urodela, as it is not derived from the hyomandibula. There is, however, as yet, no general agreement on this latter point for, while Tumarkin (1948 a, b) supports Gaupp's findings (1896–1904) that the anuran columella auris is a derivative of the auditory capsule, a number of authors, including Gazagnaire (1932), de Beer (1937), Westoll (1943), Witschi (1949, 1956) and Cordier & Dalcq (1954), conclude that it is a modification of part of the hyoid skeleton.

It is also apparent from the literature that in the Anura the middle ear is structurally somewhat variable and this may partly be responsible for the

conflicting ideas regarding the origin of its constituent parts. While the majority of the species investigated have a complete auditory mechanism and are thus assigned to Tumarkin's (1948 a) vestibulo-tympanic category, occasionally, as in *Hemisus* (de Villiers, 1931), the Leiopelmidae (de Villiers, 1934 ; Wagner, 1934/35 ; N. G. & E. M. Stephenson, 1951), *Bombina* (Slabbert, 1945) and a few other genera, only the operculum is present and they all presumably have recourse to the vestibulo-scapular method described by Tumarkin (1948 a). In this they resemble the more erect Urodela and, consequently, there has been some interesting speculation as to the significance of such a deviation from the more usual anuran condition. While it seems to be agreed that the absence of the middle ear in these particular Anura is an indication of adaptation for terrestrial life or even more specifically a modification resulting from fossorial habits, as suggested by Eiselt (1941), the problem of whether it represents a primary condition or a secondary loss is difficult to resolve. Thus, whereas de Villiers (1934) and Slabbert & Maree (1945) suggest that the parts may have disappeared in the course of evolution, N. G. Stephenson (1951) is of the opinion that the absence of the middle ear in Urodela and the Leiopelmidae depicts the initial stage. There is much in favour of both viewpoints for, while the contentions of the former authors seem to be supported by palaeontological evidence, N. G. Stephenson's conclusions (1951) seem equally justifiable. It is a well-known fact that in Anura the parts of the middle ear only appear during metamorphosis and, apart from N. G. Stephenson's (1951) careful observations on the ontogeny of *Leiopelma archeyi*, there is no information concerning the development of any of the interesting species of Anura that lack the middle ear. It is, therefore, rather significant to note that no traces of the auditory columella can be detected at any stage in *Leiopelma archeyi*, and it seems reasonable to suppose that, as in the Urodela, there is some evidence of neoteny, rather than of secondary loss.

At the same time, however, the Stephensons (N. G., E. M., 1951) have identified a procartilaginous structure in *Leiopelma* with the primitive hyomandibula, and find that one of its derivatives, the hyobasal, suspends the quadrate to the neurocranium. For this reason they do not subscribe to Tumarkin's views (1948 a) regarding the disappearance of the hyomandibula in the Anura. Their findings suggest that in the Leiopelmidae, and perhaps in other frogs lacking the middle ear, the hyomandibula, if present, has assumed a different function. It must be remarked, however, that the writer's preparations of *Xenopus* and other Pipidae show no evidence of a hyomandibula. Although the middle ear differs somewhat from that of *Rana*, described by Gaupp (1896–1904), and a small operculum is only present in *Xenopus*, the indications are that both it and the columella develop in close association with the auditory capsule. To some extent, the observations on the Pipidae support Tumarkin's conclusions (1948 a) and also those of Eiselt (1941), who considers that the Amphibian operculum is a detached portion of the wall of the auditory capsule.

Notwithstanding the controversial problems concerning the homology of the auditory columella, it is apparent that opinions relating to sound reception and perception in adult Anura are becoming more concrete and coherent.

Contrasted with this, there is but little information regarding hearing during larval life and, apart from several embryological and morphological studies, the physiology of the larval ear has been largely neglected due, no doubt, to difficulties involved in the interpretation of results of experiments on larval specimens. Herter's observations (1921) are therefore, rather unique in that they cover, not only the development and morphology of several species, but also describe the results of patient experimental investigations on young frogs and different stages of larvae. His work, however, in common with most of that pertaining to adult Anura, deals essentially with the non-acoustic part of the labyrinth, regarding which the post-operative results are more clearly evinced than are those of the areas generally assumed to be auditory in function.

The method of sound perception in larval Anura is thus not fully understood and is still a matter of speculation. The tadpoles of the majority of frogs are aquatic and it might be supposed that either a temporary vestibulo-squamosal, as in aquatic Urodela, or a vestibulo-scapular arrangement, as in *Bombina*, would precede the perfected vestibulo-tympanal mechanism of the adult but, so far, this has not been demonstrated. Judging from developmental stages of *Xenopus laevis*, the parts of the inner ear are almost perfectly arranged in larvae of 16 mm. (Paterson, 1949) or in slightly older larvae of 20–27 mm. (Nieuwkoop & Faber, 1956). The middle ear, however, only makes its appearance during metamorphosis and, in its absence, there is no clear indication as to the means of sound reception and conduction in pre-metamorphic stages. In any case, it seems that even in adult frogs the middle ear is not necessarily a requisite of the hearing mechanism, for physiological texts such as Prosser (1952) quote Yerkes (1905) as having successfully demonstrated that the frog's ear was still receptive after extirpation of the tympanum and the columella. Yerkes' contention that frogs have a fairly good sense of hearing is indirectly supported by the experiments of Ferhat-Akat (1939), who succeeded in training various urodeles to respond to sounds of different pitch and frequency, but his results also demonstrate that, as in fishes (von Frisch, 1936, 1938), the lower notes are probably perceived by the skin receptors. In contrast to these views, Adrian, Craik & Sturdy (1933) believe that the frog's ear is primarily sensitive to mechanical vibrations and is otherwise only stimulated by very loud noises. Thus, although opinions are varied and somewhat conflicting, they do suggest that the amphibian ear reacts to vibratory stimuli, some of which are probably auditory. From this it may be inferred that their larval forms, although apparently unresponsive to loud sounds, are nevertheless, capable of distinguishing different kinds of stimuli. As may be readily observed, either in nature or in the laboratory, the larvae of *Rana* and *Xenopus*, by their immediate response to any unusual disturbance of the water, are undoubtedly sensitive to vibrations in the water, but it is difficult to ascertain from their reactions if the ears are actually phonoreceptive. That the lateral-line organs are responsible to some extent for this acute sensitivity to mechanical stimulation seems to be established by the experiments of Kramer (1932/33) on adult *Xenopus laevis* and those of Sand (1937)

on fishes, while the probability that these organs participate in the reception of sound waves has recently been maintained by Pumphrey (1950). As yet, no experimental proof has been given of auditory receptors in larval Anura, but certain studies of the morphological details of the ear and related structures have produced some ideas with a direct bearing on the problem.

As early as 1902, Harrison, in his comprehensive investigation of the perilymphatic system of various Amphibia, revealed that in the larvae of *Rana temporaria*=(*fusca*) and *Pelobates fuscus* the bronchus and lung, respectively, are connected on each side to the ventral wall of the corresponding saccus perilymphaticus by a dense fibrous strand. Relative to this discovery he made the following interesting remarks (p. 244), "I would venture to suggest that the arrangement be compared with the connection of the air bladder with the auditory capsule, which is found in some fishes (Weberian ossicles). At any rate, there is obviously here a very efficient apparatus for passing on changes of pressure within the lung along the dense fibrous column to the membrane of the saccus perilymphaticus and thence by the recessus partis basilaris to the interior of the pars basilaris itself. *It seems probable that the function of the apparatus is intimately connected with the aquatic mode of life.* The lungs at this stage are functional in part as swim bladders and the variations of pressure within their cavities is, no doubt, partly dependent on the hydrostatic pressure".

Although Gaupp (1904) suggested that Harrison's disclosure warranted further investigation, its significance does not seem to have been fully appreciated. Quite recently, however, Witschi (1947, 1949, 1955, 1956) has described a similar arrangement in larvae of different species of *Rana*. He defines the fibrous connexion between the bronchus and the 'round window' at the back of the auditory capsule as a 'bronchial columella' and considers that it is of special importance in transmitting sound vibrations from the lungs to the inner ear. He further supports his contention (1950) that the lungs of larval frogs are auditory receptors by comparing the conditions in *Rana* with those of *Xenopus*. The bronchial diverticula of the latter have previously been described and tentatively associated with the hydrostatic function by Weisz (1945), but Witschi now places them with the bronchial structures of *Rana* in the category of subsidiary hearing organs. In lacking fibrous columellae, the system of *Xenopus* is regarded by Witschi (1950) as being less specialized than that of Ranidae, in at least six species of which he has recorded (1955) the extraordinary events culminating in the temporary enclosure of the columellae in the dorsal aortae and their subsequent disappearance at the end of metamorphosis.

There can be little doubt as to the close resemblance between the bronchial appendages in tadpoles of *Rana* and *Xenopus*, and the fact that they project towards the occipital condyles and become approximated to the more superficial part of the perilymphatic system seems to suggest some connexion with the functions of the ear. In *Xenopus*, at least, their development coincides with the completion of the inner ear but, as in *Rana*, they are transitory larval structures that vanish during metamorphosis. According to the Normal

Table of *Xenopus laevis* (Nieuwkoop & Faber, 1956) they appear at Stage 50 in larvae measuring 20–27 mm., by which time all the parts of the inner ear are delineated. There may, however, be some slight variation in the sequence, for in serial sections of this species, kindly placed at my disposal by Dr N. A. H. Millard, of this Department, the bronchial outgrowths (br. div. Fig. 1) are only first apparent in larvae measuring 37 mm. and comparable in development to about Stage 52 in the Normal Table. They are better differentiated in 44 mm. larvae, in which they resemble those described and figured by Weisz (1945) in his third-form tadpole.

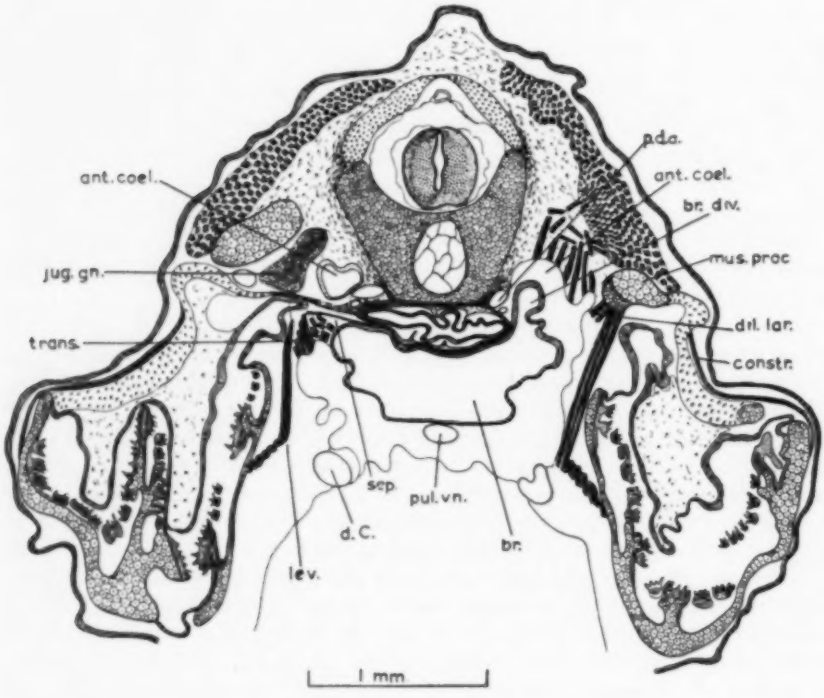


Fig. 1.—*Xenopus laevis*. T. S. posterior region of head of 37 mm. larva, showing bronchial diverticulum lying in anterior part of coelom. (Key to lettering, p. 545.)

The presence of these bronchial structures in larval frogs thus appears to be highly significant, more especially if they are instrumental in conducting stimuli to the inner ear. If, however, their purpose is auditory as Witschi (1947–56) suggests, it is somewhat difficult to understand how larvae detect sounds prior to their development and how, on the assumption of the vestibulo-tympanic mechanism at the critical time of metamorphosis, the complete reversal in the direction of vibrations passing through the ear is accomplished. It is, nevertheless, an interesting theory, and one which Witschi has hinted

(1955) will later be supported by experimental proof concerning the function of the ' bronchial columellae '.

It is evident from the foregoing remarks that the amphibian ear has been a profitable subject for both structural and functional investigations. Among Anura, that of *Rana* is probably the best known, but the morphology of the ear of other species has also received attention. The ear of the adult *Ascaphus truei* has been described and contrasted with that of other genera by de Villiers (1934). A further account of the inner ear of this species and that of *Leiopelma hochstetteri* has been given by Wagner (1934/35), who has also discussed the implications of the absence of the middle ear in these forms. Information concerning the auditory region of the Pipidae has likewise been accumulating, for, in addition to the details of the middle ear of *Pipa*, *Hymenochirus* and *Xenopus*, supplied by de Villiers (1932), the writer has reported on the development of the inner ear of *Xenopus* (1949) and on the middle ear of an adult *Hemipipa* (1955).

The Pipidae comprise an interesting assemblage of aglossal forms, generally assumed to be wholly aquatic, but Dunn (1948) has indicated that *Pipa pipa* and *Hemipipa carvalhoi* occasionally migrate on to land while, according to Johnson (1952), the latter species is capable of surviving drought periods by burying in mud to a depth of two feet. Dunn's suggestion (1948), that all the American species be relegated to the genus *Pipa*, would entail the suppression of the genera *Protopipa* and *Hemipipa*, but as the latter name is in general use, it has been retained in the present and previous articles by the writer. The species included in the family are somewhat heteromorphic and present such a variety of characters that it is almost impossible to obtain a clear impression of their interrelationships. Dunn (1948) considers that the American and African species form two natural groups, but it must be admitted that the African genera, *Xenopus* and *Hymenochirus*, although apparently having a similar life history, are almost as different anatomically from each other as each is from any of the American species. While Noble (1931) has concluded that, in respect of certain skeletal features, *Hymenochirus* ranks as the most specialized of all the Pipidae, some authorities consider that *Xenopus* is the most primitive member of the family. It is rather significant, however, that each species presents definite and usually different evidences of neoteny and, if it were possible to relate these to ' primitive ' or ' specialized ' features, some of the apparent anomalies regarding the affinities of the family might be more intelligible.

As has been indicated above, the middle ear of the better known Pipidae has been fully investigated and some details of the inner ear of *Xenopus laevis* have also been disclosed. The present observations are intended to give an impression of some anatomical variations of the inner ear noticed in the course of studies of the cranial morphology of members of the family and, as far as possible, an attempt has been made to correlate the findings with conditions in other Anura.

The material studied consists of serial sections of the heads of adult *Hemipipa carvalhoi* Mir.-Rib., *Hymenochirus curtipes* Noble and *Xenopus*

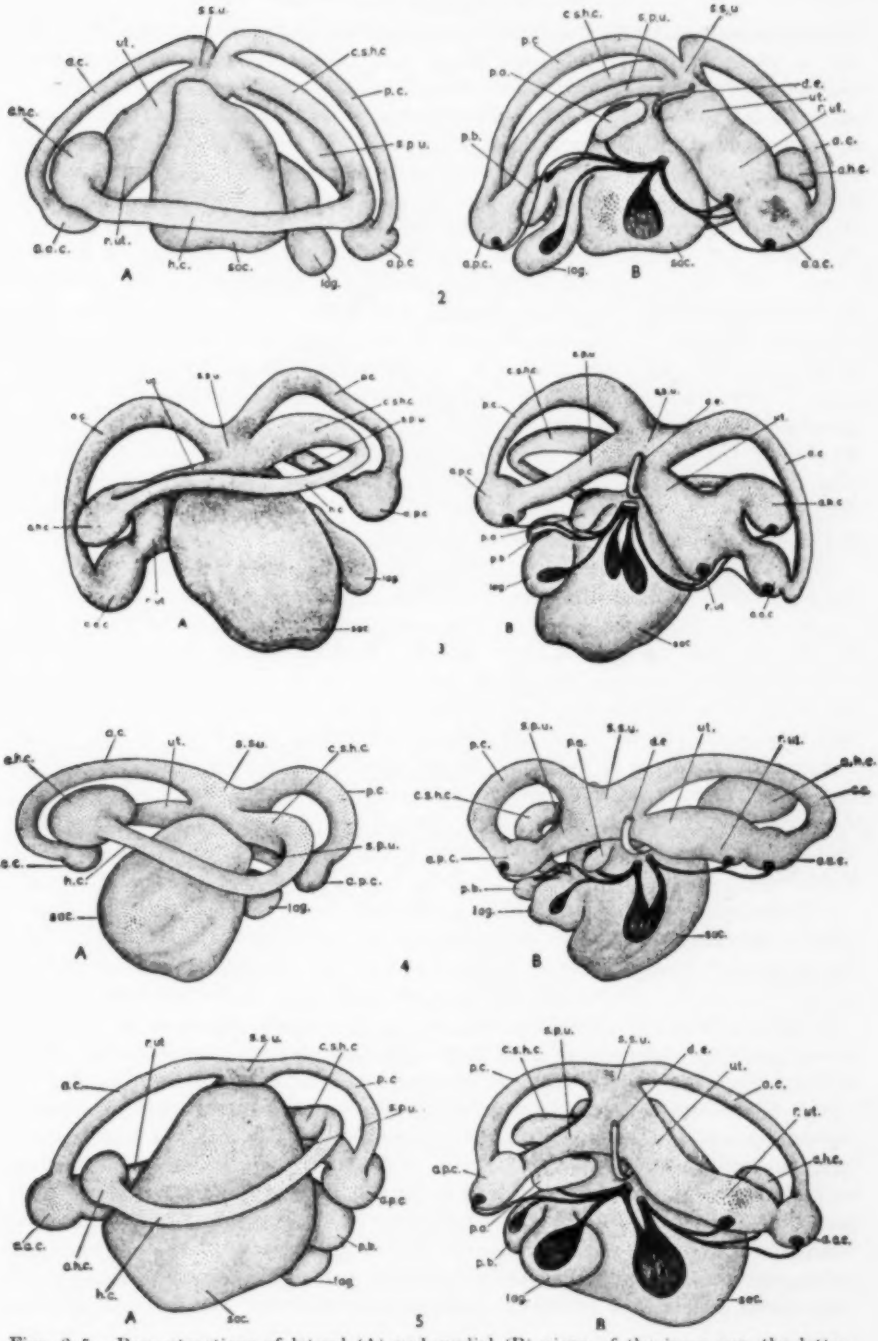
laevis Daudin, in addition to young *Pipa pipa* Linné, various larval stages of *Xenopus laevis* and one-day-old larvae of *Hemipipa carvalhoi*. In view of Witschi's recent interpretation (1947–56) of the structures in *Rana* and *Xenopus*, larval stages of *Rana fuscigula*, collected locally, were sectioned for comparison with the other species.

COMPARATIVE ACCOUNT OF THE PIPID INNER EAR

Structurally the ear of representatives of different families of Anura appears to be remarkably uniform, and the main variations so far recorded apply more especially to the middle ear and to certain particulars of the distribution of the branches of the auditory nerve to the membranous labyrinth. The dissimilarities of the sound-transmitting apparatus of the Pipidae and other Anura have been discussed in a number of publications by de Villiers (1931, 1932, 1934), who, from his wide experience of anuran cranial anatomy, speculates as to the reasons for the variability of the parts and the absence of the middle ear in some species.

Unlike the middle ear, the membranous labyrinth of Anura has aroused little attention and, of the Pipidae, only that of *Xenopus* has, as yet, been studied in some detail (Paterson, 1949 ; Nieuwkoop & Faber, 1956). The present observations indicate that, while in section the component parts may seem to be diversely arranged, the configuration of the organ as a whole is essentially similar in the four species investigated when reconstructed either graphically or by means of wax models. This is hardly unexpected for, throughout the Anura, the labyrinth is subjected to few modifications, and the most striking differences between the pipid condition and that of the better known *Rana* are associated with the posterior part of the perilymphatic system and with the absence of the tegumentum vasculosum. According to de Villiers (1934) and Wagner (1934/35), the latter organ is also lacking in the Leiopelmidae and, while it has no apparent counterpart in any of the Pipidae, it may be noted that the dorsal part of the sacculus of *Xenopus* and of one-day-old larvae of *Hemipipa* is heavily pigmented. In premetamorphic specimens of *Rana fuscigula* the tegumentum vasculosum develops as a lateral extension of the upper part of the sacculus, which becomes more conspicuous and applied to the dorso-lateral wall of the pars basilaris during metamorphosis. Although its function is obscure, Gaupp (1904) has indicated that it was considered by early investigators to correspond to the tegumentum vasculosum (membrana Reissneri) of amniotes. If it is analogous to the stria vascularis of the mammalian labyrinth, it may be regarded as an adaptive feature for secretion or even absorption, which, for some reason, is not required in the Leiopelmidae and Pipidae.

The general similarity in the disposition of the parts of the labyrinth in the four species of pipids is evident in Figs. 2 to 5, and, as the arrangement conforms closely to that of other Anura, only a brief description is necessary. The pars superior, comprising the main static portions of the labyrinth and consisting of three well-defined semicircular canals and the utriculus, is readily distinguished from the components of the pars inferior, which are generally supposed to function in sound perception. Each semicircular canal has a



Figs. 2–5.—Reconstructions of lateral (A) and medial (B) views of the inner ear, the latter depicting the approximate course of the ramuli of the auditory nerve. (Key to lettering, p. 545.) Fig. 2.—*Pipa pipa*. × 20. Fig. 3.—*Hemipipa carvalhoi*. × 16·6. Fig. 4.—*Hymenochirus curtipes*. × 20. Fig. 5.—*Xenopus laevis*. × 20.

conspicuous ampulla with a large crista acustica. In some sections (Fig. 6) and in views of the whole organ (Figs. 2–5) the adjacent ampullae (a.a.c., a.h.c.) of the anterior vertical and horizontal canals may be seen communicating with the recessus utriculi (r. ut.), which is distinguished from the more dorsal utriculus (ut.) by its obvious macula utriculi (m.ut. Fig. 6), resting on which is a thin, flat otolith. The recessus utriculi seems to be proportionally larger in *Pipa* and *Hemipipa* than in *Hymenochirus* and *Xenopus*, and in all of them, dorsal to the wide utriculus, is the sinus superior utriculi (s.s.u. Figs. 2–5, 10), formed by the union of the anterior and posterior vertical tanals. The horizontal canal (h.c.) establishes a posterior connexion with the utriculus by means of a wide crus simplex (c.s.h.c.), while at approximately the same level the sinus posterior utriculi (s.p.u.) from the posterior vertical canal (p.c.) also joins the utriculus. In section the sinus posterior utriculi and the crus simplex of the horizontal canal appear as adjacent cylinders directed obliquely upward towards the utriculus and, whereas in *Hymenochirus* the former tends to remain medial to the crus simplex for most of its extent (Fig. 7), in the other three species it assumes a more ventro-medial position (Fig. 8), except in the Stellenbosch series of *Pipa* (Fig. 9), where some similarity to the arrangement in *Hymenochirus* is evident.

The largest part of the pars inferior is, of course, the sacculus, of which the other three organs, the lagena, the pars basilaris and the pars neglecta of Gaupp (1904) and other authors or the pars amphibiorum of de Burlet (1934), may be considered as appendages. Relative to the size of the entire labyrinth, the sacculus of *Xenopus* appears to be the most extensive, and in all four species it is characterized by a distinct median vertical macula (m.sac. Fig. 9) and a large otolith, which is particularly noticeable in sections of *Pipa* and *Hemipipa*. In none of them is the sacculus obviously divided into upper and lower regions as in *Rana* (Gaupp, 1904), but in *Hymenochirus* and *Xenopus* (Fig. 10) it is projected dorso-laterally above the level of the foramen utriculosacculare (f.u.s.) and an approach to the ranid condition may be indicated.

The lagena (lag. Figs. 2–5, 7, 8) is a relatively large, posterior, oval evagination of the sacculus in which the otolith is less conspicuous than that of the sacculus. Its macula (m.lag. Figs. 7, 8) is well marked and, although slightly variable in position, is predominantly medio-ventral in all four species.

The pars basilaris (p.b. Figs. 2–5, 8, 11, 12), which distinguishes the ear of the majority of Amphibia from that of Pisces, is a postero-dorsal outgrowth of the lagena, but it also communicates widely with the sacculus. It is provided with a sensory papilla but, unlike the sacculus and lagena, it has a tectorial membrane and no otolith. Moreover, it lies close to the ductus perilymphaticus and, at its point of contact with the latter, its otherwise remarkably thick wall becomes noticeably thinner to form a delicate vertical partition (Fig. 11) separating perilymph from endolymph. As the papilla basilaris is recognized as the forerunner of the organ of Corti of more specialized tetrapods, this region is generally regarded as the chief acoustic centre in Amphibia, but Hilton (1952) has suggested that there is reason to believe

that the pars amphibiorum, which is exclusive to this class, may be of greater significance in this connexion.

In the four species of pipids examined, the pars amphibiorum (p.a. Figs. 2–5, 7, 12) is well defined and is pronounced in *Pipa* (Fig. 9), where it is pro-

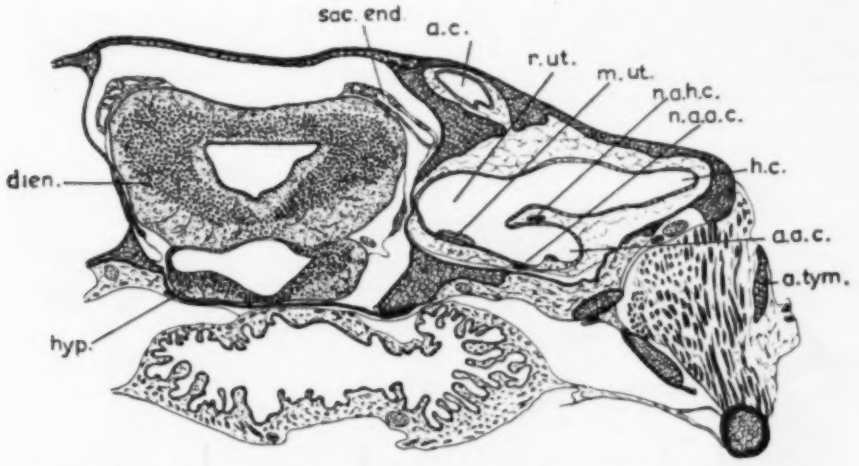


Fig. 6.—*Pipa pipa*. T. S. anterior region of inner ear × 30. (Key to lettering, p. 545.)

portionally more voluminous than the pars basilaris. Rough estimates of the ratio of the two parts to each other indicate that, while in *Hymenochirus* and *Xenopus* the pars amphibiorum is respectively three-quarters and one-half the size of the pars basilaris, in *Pipa* it is 1·6 and in *Hemipipa* 1·2 times larger. The significance of these differences is not clear but if, as is usually supposed, the pars basilaris of Anura is of more import in sound detection than the pars amphibiorum, it seems to imply that *Hymenochirus* and *Xenopus* have greater acuity of hearing, even though they are more entirely aquatic than the other two species. At the same time, it may also indicate that *Pipa* and *Hemipipa* are closer to the urodele condition in which, as may be gathered from the remarks of Harrison (1902) and Hilton (1952), the pars basilaris appears to be of less functional importance than the pars amphibiorum.

In all of them the pars amphibiorum is in wide communication with the medio-dorsal wall of the sacculus (Fig. 9) and occurs immediately behind the level of the foramen utriculo-sacculare (f.u.s. Fig. 10) and the origin of the ductus endolymphaticus (d.e. Fig. 10) from the sacculus. Associated with the papilla amphibiorum, which marks its dorsal wall, is a conspicuous, more or less S-shaped tectorial membrane (indicated in Figs. 9, 12), while postero-ventrally the dividing wall between the pars amphibiorum and the ductus perilymphaticus is very thin. This partition and also that connected with the pars basilaris have been termed ' tympanal areas ' by Harrison (1902), who has discussed their probable significance in the transmission of vibrations from the perilymphatic to the endolymphatic system. Similar conclusions have also

been reached by de Burlet (1934), but in deliberating on the position of these membranes relative to the sensory endings in the partes basilaris and amphibiorum of *Rana*, he has further suggested that the former may also be concerned with the perception of pressure variations in the brain and the jugular vein.

Before passing to other particulars relating to the labyrinth, it may be of interest to note that one-day-old larvae of *Hemipipa* are developmentally more advanced than those of *Xenopus*. Externally they closely resemble the

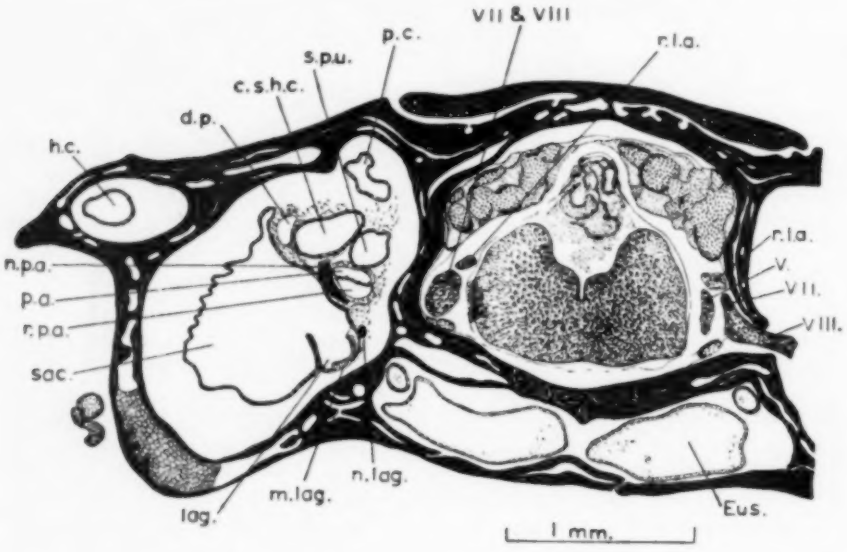


Fig. 7.—*Hymenochirus curtipes*. T. S. passing through right foramen acusticum posterior, and showing the relative positions of the crus simplex canalis horizontalis and sinus posterior utriculi on left. (Key to lettering, p. 545.)

recently hatched larva figured by de Carvalho (1939) and, perhaps due to the fact that they undergo a partial incubation on the back of the parent, they appear equivalent to Stage 46 in the normal development of *Xenopus* (Nieuwkoop & Faber, 1956), which is four days and ten hours old. The labyrinth also develops more rapidly than that of *Xenopus*, and presents similarities to that of Stage 50 in the Normal Table (Nieuwkoop & Faber, 1956). All the parts of the inner ear are established ; the anterior and posterior vertical canals are partially enclosed in cartilage and the foramen endolymphaticum is distinct from the foramen acusticum. The main differences between this and the adult condition are that the pars amphibiorum and the pars basilaris are less distinct and, as the ductus perilymphaticus is relatively short and straight, there are no obvious recesses on its course and the ' tympanal areas ' are hardly defined.

INNERVATION OF THE LABYRINTH

In all the Pipidae examined the auditory nerve (VIII, Figs. 9, 10) issues dorso-laterally from the medulla oblongata in close proximity to, but slightly behind the roots of VII and the ramus lateralis anterior, a feature which has been admirably illustrated by van der Horst (1934) in sections of the brain of *Xenopus laevis*. Although van der Horst seems to have concluded that the auditory nerve of this species has a single, very broad root, it appears from the present material that in the Pipidae there are indications of antero-ventral and postero-dorsal tracts, comparable to the anterior and posterior radices

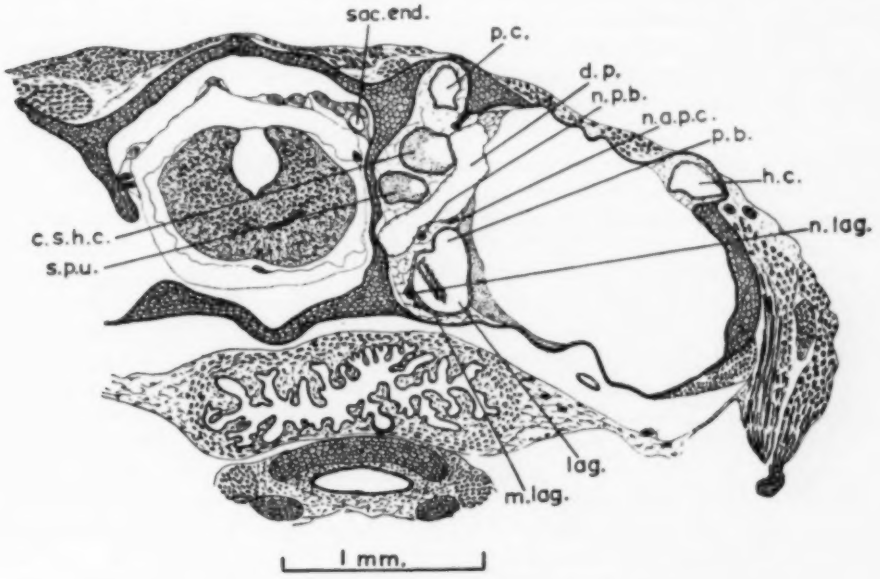


Fig. 8.—*Pipa pipa*. T. S. of parts somewhat similar to those in Fig. 7. (Key to lettering, p. 545.)

described by Gaupp (1899, 1904) and Norris (1913) in other Amphibia. Moreover, the auditory nerve emerges at a level between the root of the ramus lateralis anterior and the sensory root of VII and, while the former (r.l.a. Figs. 7, 10) remains distinct, the roots of VII and VIII combine into a large ganglionic mass (VII & VIII, Fig. 7), of which the sensory and motor constituents of VII form a small medial portion. Careful scrutiny of the sections suggests that, despite their close association, there is probably no intermingling of the facial and auditory elements. The facial nerve passes through the acoustico-facial complex and courses forward within the cranium to join the ramus lateralis anterior and the trigeminal in the conspicuous ganglion prooticum commune. The nerve supply to the labyrinth is consequently derived entirely from VIII and, as the partes superior and inferior are innervated respectively from the antero-ventral and postero-dorsal roots, it almost appears as though there is some correlation between this separation of the

two roots and differences in the physiology of the two parts of the labyrinth. This, however, is hardly borne out by the disclosures of McNally & Tait (1925–26) and MacNaughton & McNally (1946) in *Rana* and those of Lowenstein & Roberts (1948, 1950, 1951) in *Raja*, in which both equilibrial and vibrational receptors occur in the pars inferior of the labyrinth. Nevertheless, the presence of an acoustico-facial complex and the peripheral distribution of the dorsal and ventral fibres of VIII to the two regions of the labyrinth appears to be fairly general throughout the vertebrates and, although no attempt was made to study the full details, a comparison of preparations of Pipidae with sections of *Rana fuscigula* larvae, reveals a similar general plan in the relations of the ganglia and nerves.

Most students of anuran cranial anatomy incline to the view that there are anterior and posterior acoustic ganglia associated with the two main rami

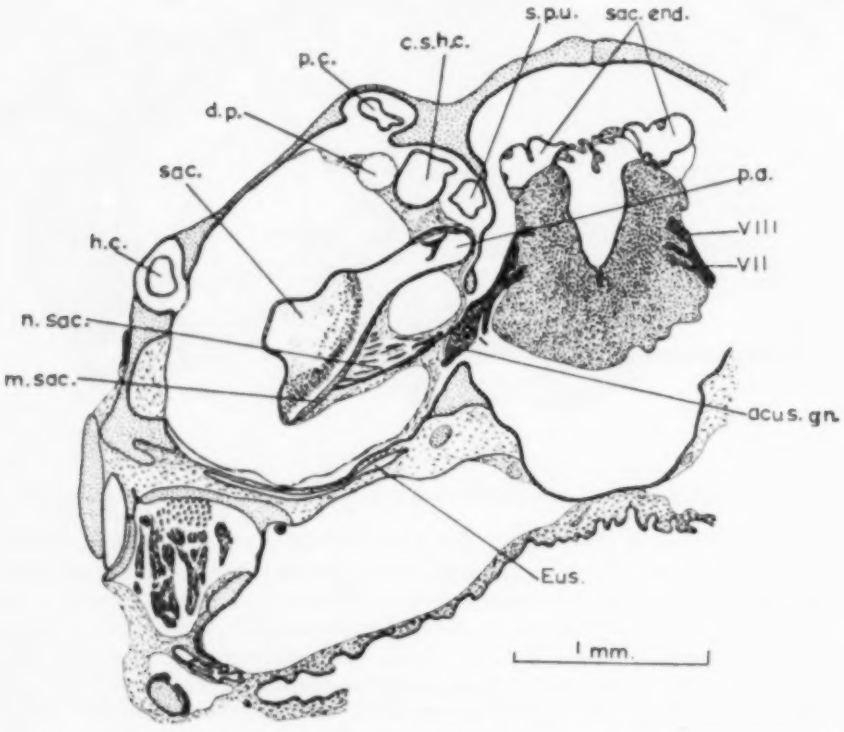


Fig. 9.—*Pipa pipa*. T. S. illustrating the single foramen acusticum and the conspicuous pars amphibiorum. (Key to lettering, p. 545.)

of the auditory nerve, but in the Pipidae, at least, it seems more appropriate to describe a single, continuous ganglion in which, for convenience, different regions, rather than discrete ganglia, may be recognized opposite the acoustic foramina. The concept of a single acoustic ganglion is readily acceptable in

Pipa and *Hemipipa*, which have a single wide acoustic foramen (Fig. 9) through which the various branches are distributed to the labyrinth. *Xenopus* and *Hymenochirus*, however, agree with *Rana* and many other Anura in having two acoustic foramina for the transmission of the main anterior and posterior nerves which, as in *Pipa* and *Hemipipa*, issue at different levels from the single acoustic ganglion.

In each class of vertebrates there seems to be some variability regarding the number of branches of the auditory nerve, some species having three and others two main factors. Among Amphibia, the Urodela generally have three branches and the Anura two, but the end result of their distribution to the sensory areas of the labyrinth is fundamentally constant. The anterior and posterior branches pass respectively to the pars superior and the pars inferior, the former supplying the anterior and horizontal ampullae and the recessus utriculi, while the posterior ramus terminates in the lagena, the pars amphibiorum, the pars basilaris and the posterior ampulla.

It is only the sacculus that has a variable supply and, as de Burlet (1934) has shown in his comprehensive survey of the vertebrate ear, it may be innervated from either the anterior or the posterior branch or from a separate median branch, or even by a combination of fibres from any of these three sources.

Although there is some slight variation in the precise distribution of the fibres to the macula sacculi in the Pipidae, it appears that they usually separate from the middle region of the acoustic ganglion between the main anterior and posterior branches and, even though there are normally never three acoustic foramina, the arrangement is reminiscent of that of Urodela and of such Anura as *Ascaphus truei* (de Villiers, 1934) and *Leiopelma* (Wagner, 1934/35), which have a median foramen for the passage of the saccular nerve. Thus, in *Pipa* (Fig. 2 B) there is a single distinct median saccular nerve, while in *Hemipipa* (Fig. 3 B) the anterior and posterior areas of the macula sacculi are innervated by two separate median nerves. The condition in *Hymenochirus* and *Xenopus* (Figs. 4 B, 5 B) is probably a modification of the *Hemipipa* system, but is complicated by the presence of two acoustic foramina, through both of which fibres pass to the sacculus. A somewhat similar conclusion is reached in the Normal Table of *Xenopus* (Nieuwkoop & Faber, 1956), where the sacculus is described as being innervated by an 'intermedial portion' of the auditory nerve. In this connexion it may be mentioned that in a few larval stages and in one postmetamorphic specimen of *Xenopus* there is on both sides a very small median acoustic foramen for the transmission of some of the more posterior fibres to the sacculus. This condition, although interesting, must be abnormal, for developmentally there is initially a single acoustic foramen which subsequently becomes divided into the separate anterior and posterior foramina of the adult.

In having what may be regarded as a median saccular nerve, the pipids differ from *Rana*, where the supply to the sacculus is generally considered to be derived from the anterior branch of the auditory nerve. Probably little significance attaches to this feature, but it would appear from de Burlet's account (1934) of the variations in the innervation of the sacculus that the

ranid condition is rather exceptional and occurs in no other vertebrate class. It seems clear, however, from the present observations that in the Pipidae, irrespective of whether the saccular nerve is given off directly from the middle of the acoustic ganglion as in *Hemipipa* and *Pipa* (n.sac. Fig. 9), or whether it is distributed through both the anterior and posterior acoustic foramina, as in *Hymenochirus* and *Xenopus* (Fig. 10), its fibres are traceable to the postero-dorsal root of VIII. Furthermore, the arrangement in tadpoles of *Rana fuscigula* is comparable to that of the Pipidae for, although the saccular nerve

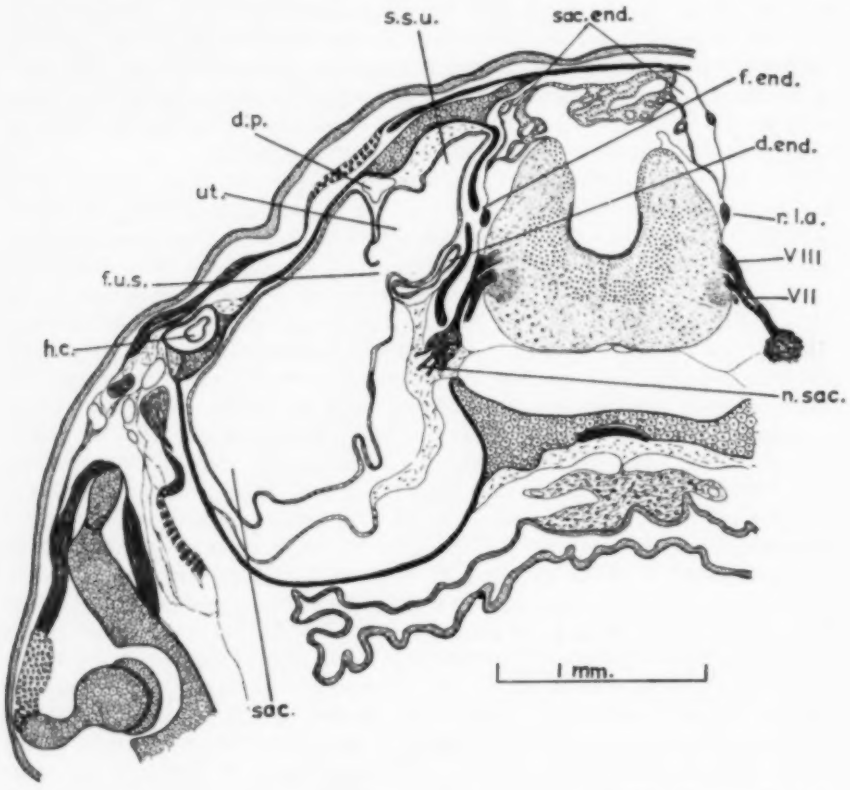


Fig. 10.—*Xenopus laevis*. T. S. of postmetamorphic specimen at level of foramen utriculo-sacculare and foramen acusticum posterior. (Key to lettering, p. 545.)

passes through the anterior acoustic foramen and represents a branch of the anterior auditory nerve, it is in reality a derivative of the postero-dorsal root of VIII.

Apart from the supply to the sacculus, the innervation of the rest of the labyrinth of pipids (Figs. 2 B–5 B) is constant and essentially similar to that of *Rana* (Gaupp, 1904) and other Anura. Thus the anterior branch divides

into three ramuli to supply the recessus utriculi and the anterior and horizontal ampullae (n.a.a.c., n.a.h.c. Fig. 6). The first ramulus of the posterior branch is a short, stout nerve to the macula lagena (n.lag. Figs. 7, 8), posterior to which the main branch continues laterally giving off another conspicuous ramulus (n.p.a. Fig. 7), which travels upward behind the pars amphibiorum to supply the dorsal papilla of this organ. The remainder of the posterior branch proceeds posteriorly, parallel to the ductus perilymphaticus, and gives off factors (n.p.b., n.a.p.c. Fig. 8) to the papilla basilaris and the crista of the posterior ampulla.

ENDOLYMPHATIC SYSTEM

As the progressive development of this system has previously been traced in various stages of *Xenopus laevis* (Paterson, 1949 ; Nieuwkoop & Faber, 1956), it is only necessary to comment briefly on the arrangement in the other three species of Pipidae herein considered.

In common with other Amphibia, the system is well developed and bilaterally symmetrical. It consists of a pair of intracranial sacci endolymphatici (sac.end. Figs. 6, 8–10), lying dorso-laterally over the brain and communicating on each side with the inner ear by means of a relatively wide ductus endolymphaticus which enters the cranial cavity through the foramen endolymphaticum. The latter is located on the medial wall of the auditory capsule, immediately antero-dorsal to the posterior acoustic foramen in *Hymenochirus* and *Xenopus* (f.end. Fig. 10) and above the anterior margin of the single acoustic foramen in *Pipa* and *Hemipipa*. In all of them the ductus endolymphaticus (d.e. Figs. 2 B–5 B, 10) originates in the medio-dorsal angle of the sacculus close to the foramen utriculo-sacculare (f.u.s. Fig. 10) and passes medially beneath the utriculus to proceed obliquely upward to the foramen endolymphaticum.

The main variations in the system relate to the length and lobulations of the saccus endolymphaticus. Of the four pipids investigated, it is most extensive and complicated in postmetamorphic stages of *Xenopus*, where it not only has a considerable intracranial portion but is also continued posteriorly into the neural canal and terminates beyond the fourth intervertebral foramen.

The condition in one-day-old larvae of *Hemipipa* is extremely simple and resembles that of a 16 mm. larva of *Xenopus* (Paterson, 1949) in that the sacci endolymphatici are undivided and located over the anterior two-thirds of the hind brain. The sacci almost meet mid-dorsally and, as the ducti endolymphatici communicate with them mid-laterally, definition is given, even at this early stage, to the anterior and posterior parts of the system.

In sections of young *Pipa* the sacci endolymphatici (sac.end. Figs. 6, 9) are also clearly defined between the dorsal dural veins and the brain, but in adult *Hemipipa* and *Hymenochirus* the walls of the sacci are very delicate and difficult to trace. It is evident, however, that in these adult specimens and also in the young *Pipa* the pars anterior has become progressively more extensive and more lateral in position than in the initial stage seen in *Hemipipa* larvae. Furthermore, it is divisible into dorso-lateral and ventro-lateral

compartments, especially in the region of the large ganglion prooticum commune and the hypophysis, but in none of them is there any intercommunication between right and left halves. In all three species this anterior part of the saccus extends along the telencephalon, terminating anteriorly at about the posterior quarter of the cerebral hemispheres in *Pipa* and *Hemipipa* but in *Hymenochirus*, where the system is rather more attenuated, it continues about halfway along the hemispheres.

Behind the ductus endolymphaticus the pars posterior of each saccus endolymphaticus arches over the brain and is closely apposed to the chorioid plexus of the fourth ventricle. In *Pipa*, as in *Xenopus* (Fig. 12 D), this portion tends to be more lobular than the pars anterior and at least three diverticula are developed among the dorsal dural veins ; in *Hemipipa* and *Hymenochirus*, although it may be irregularly constricted, discrete lobes are not apparent.

Towards its posterior limit each saccus endolymphaticus gradually narrows and assumes a more lateral position. In *Pipa* it extends down five-sevenths of the length of the medulla oblongata (sac.end. Fig. 8), and in *Hemipipa* it also ends near the posterior extremity of the brain. It seems to be rather longer in *Hymenochirus*, for traces of it were observed over the first spinal ganglion, to which level the series of sections was taken.

From the foregoing it is apparent that in *Pipa* and *Hemipipa* the sacci endolymphatici are confined to the cranial cavity and, in this respect, resemble those of Urodela and of *Bombina* and *Discoglossus* among Anura (Whiteside 1922 ; Noble, 1931). It has been suggested by the latter author that the absence of the spinal portion of the system in urodeles " is correlated with the poor auditory powers in this group " (p. 338). As, however, Ferhat-Akat (1939) has provided experimental evidence that urodeles are not only sensitive to sound, but can also distinguish differences in musical pitch, it seems rather doubtful if, as may be inferred from Noble's statement, the pars spinalis characteristic of Anura contributes towards an increased acuity of hearing. In fact, although developmental and morphological studies have resulted in a better understanding of the system, its specific function remains uncertain.

Associated with the spinal portion observed in certain Anura are paired intervertebral sacs containing calcareous concretions. Similar sacs are also developed in *Xenopus*, while the presence of calcareous matter in the pars anterior of the saccus endolymphaticus of Pipidae in the vicinity of the ganglion prooticum commune is another feature in agreement with the conditions in *Rana* and other Anura reported by Whiteside (1922) and Dempster (1930). In reviewing the various theories regarding the probable function of the system, these two authors have indicated that a few authorities subscribe to the opinion that the intervertebral sacs serve as reservoirs of calcium carbonate that may be utilized during bone formation. Apart from Gaupp's observations (1904), there is little proof of this contention and, although Herter's findings (1921) would seem to refute it, Dempster (1930) considers that Herter's experiments lacked proper control and should be regarded as inconclusive. Just as no decision has been reached concerning this view, other theoretical

interpretations of the functional importance of the system are equally unresolved.

It may be recalled that the endolymphatic system develops as an outgrowth of the sacculus and its calcareous inclusions suggest the possibility of its participation in the static function associated more specificially with the pars superior of the labyrinth. While this is pure conjecture, it is of interest to note that Lowenstein & Roberts (1948, 1950, 1951) have demonstrated that in elasmobranchs there is evidence that the recessus utriculi is not the sole gravity receptor in the labyrinth, but that this function is shared by the macula lagenae and the posterior part of the macula sacculi. Similar interesting facts have also been revealed by McNally & Tait (1925–26) and MacNaughton & McNally (1946) in experiments on the labyrinth of *Rana*, in which it was found that the lagena, but not the sacculus, was concerned in equilibrium. Although the position of the saccular otolith in Pipidae could not be related to the innervation of the macula sacculi, it seems rather significant that the latter should be supplied by two nerves in *Hemipipa*, *Hymenochirus* and *Xenopus*. Anterior and posterior rami sacculi have also been described by Pearson (1936) in the ostariophysian genera *Ameiurus* and *Carassius* and, by analogy with Lowenstein's & Robert's findings in *Raja*, it seems not improbable that in forms with a double saccular innervation the sacculus may have a dual function as a gravity and vibrational receptor and that the endolymphatic system in Anura may be an additional part of the mechanism.

Perhaps it is also of some significance that in the Ostariophysi, which have been shown by von Frisch (1936, 1938) to react to sounds, there is a sinus endolymphaticus connecting the two sacculi. In these fishes this small intracranial endolymphatic vesicle is closely apposed to perilymphatic spaces which are in functional relationship with the Weberian ossicles and the swimbladder on each side of the anterior part of the vertebral column. It has generally been accepted by de Burlet (1934), von Frisch (1936, 1938) and others that this remarkable complex in Ostariophysi is mainly auditory, but Pearson's tentative suggestion (1936) that it may also be partly hydrostatic is confirmed in the recent review of the teleostean swimbladder by Jones & Marshall (1953), who find that, in addition to its rôle as a respiratory and a sound-producing organ, its close association with the ear in Ostariophysi may enable it to function as a manometer and as a hydrophone. Although it would be futile to attempt to correlate these findings with the arrangements in Amphibia, it seems more than coincidental that in both groups there should be a development of endolymphatic and perilymphatic spaces round the occipital region of the cranium.

That the endolymphatic system is probably of greater importance in the Anura than in other vertebrates is suggested by the fact that it reaches its maximum development in this group. The reason for this is not apparent and, while it might be deduced that the presence of voluminous endolymphatic sacs is concomitant with their amphibious habits, Dempster (1930), who investigated the structural arrangement in as many as thirty-four different

species of Amphibia, has concluded that there is no correlation between the various types of endolymphatic organs and the habits of the animals. Although he submits that the enlarged endolymphatic vesicles of Anura may be analogous to protective meninges, he favours the view that the saccus endolymphaticus is required for the release of fluid from the sacculus. It seems feasible that the system is intimately concerned with the regulation of pressure in the labyrinth, but it is more difficult to ascertain if there is any analogy between the manometric function of the Weberian apparatus of Ostariophysi and the mechanism of hydrostatic control in Anura, in which the lungs appear to be more closely related to the perilymphatic spaces than to the endolymphatic system. According to Whiteside (1922), Hasse (1873) must have been one of the first to postulate a labyrinthine pressure regulatory function for the anuran endolymphatic system, but his further suggestion that the system is a link between the skull and the ear for the transmission of sound waves appears to have found little support from subsequent observations. Most of these varied speculations regarding the function of the system are based mainly on analyses of its structural arrangement and, while none is conclusive, they suggest that the large endolymphatic sacs of Anura may subserve a combination of physiological requirements confronting animals that are amphibious in habit.

PERILYMPHATIC SYSTEM

From previous observations on the perilymphatic system of *Xenopus* (Paterson, 1949 ; Nieuwkoop & Faber, 1956), it may be concluded that, apart from some minor modifications, it is essentially similar to that of other Anura described in some detail by Harrison (1902), Gaupp (1904) and de Burlet (1934).

In all the Pipidae the perilymphatic system comprises a series of intracapsular and intracranial spaces, the largest of which (spat. sac. Figs. 12 A–D), the spatium sacculare of Harrison (1902) or the cysterna perilymphatica of de Burlet (1934), lies between the pars inferior of the labyrinth and the lateral wall of the auditory capsule. It thus adjoins the thin lateral boundary of the sacculus on the one hand and the fenestra ovalis on the other. A slight recessus fenestrae ovalis (r.f.o. Fig. 12 A) is apparent in the fossa fenestrae ovalis of *Hemipipa*, but in *Pipa*, perhaps due to the immaturity of the specimens, although the fossa itself (f.f.o. Fig. 12 B) is conspicuous, it is filled with delicate connective tissue, and there is no obvious perilymphatic recess associated with it. The condition in *Hymenochirus* is complicated by the unusual arrangement of the plectral apparatus and neighbouring parts, relative to which de Villiers (1932) has described the fossa fenestrae ovalis as lying external to the fenestra ovalis. It seems probable, however, that the auditory capsule is divisible into two regions, and that the space identified by de Villiers as the fossa fenestrae ovalis is in reality a forward projection of the posterior part of the capsular lumen, which houses the sacculus and other organs of the pars inferior of the labyrinth. If such is the case, then *Hymenochirus* (Fig. 12 C) and *Xenopus* (Fig. 12 D) differ from the other two species and resemble *Rana* in having neither a fossa nor a recessus fenestrae ovalis.

Arising dorsally from the spatium sacculare, a relatively wide ductus perilymphaticus (d.p. Figs. 7–10, 12) courses posteriorly along the side of the utriculus and for a short distance parallel to the crus simplex of the horizontal canal before passing medially between the pars amphibiorum and the pars basilaris. Towards the posterior end of the former, it forms a slight recessus partis amphibiorum (r.p.a. Figs. 7, 12), separated from the floor of the pars amphibiorum by a delicate partition or ' tympanal area '.

More posteriorly the system is rather variable and somewhat difficult to homologize with that of the Anura so meticulously investigated by Harrison (1902). Of the four species of Pipidae examined, the arrangement in *Hymenochirus* bears a close resemblance to the system in larvae of *Rana* and *Pelobates* in that, some distance behind the posterior acoustic foramen, the ductus perilymphaticus passes through the foramen perilymphaticum superius (f.p.s. Fig. 12 C) in the medial wall of the auditory capsule to join an intracranial space (spat.men.), the spatium meningeale of Harrison (1902). Almost immediately, the ductus re-enters the auditory capsule and dilates into the recessus partis basilaris (r.p.b.), which, like the recessus partis amphibiorum, is separated from the endolymphatic system by a thin-walled ' tympanal area ' at its point of contact with the pars basilaris. Assuming that the course of the ductus perilymphaticus of *Hymenochirus* is similar to that of other Anura, then a short ductus reuniens must have been established to connect the spatium meningeale and the recessus partis basilaris. Its passage through the medial wall of the auditory capsule (f.p.a. Fig. 12 C) is, therefore, probably comparable to the temporary foramen perilymphaticum accessorium, described by Harrison (1902) in *Rana* larvae, in which it subsequently becomes indistinguishable from the jugular foramen.

One of the difficulties in attempting to determine the true identity of the perilymphatic foramina in the Pipidae lies in the fact that in *Hymenochirus*, *Pipa* and *Hemipipa* the system makes its posterior exit, not directly through the floor of the auditory capsule, as in other Anura, but through the medial wall into the cranial cavity. Thus, in these three species, the posterior part of what appears to be the spatium meningeale lies below the roots of cranial nerves IX and X and extends for a short distance into the jugular foramen. In the majority of Anura the inferior perilymphatic foramen is apparently confluent with the anterior part of the jugular foramen, and a somewhat analogous arrangement may be presented by these Pipidae. As Harrison (1902) has shown, however, that it is the recessus partis basilaris that emerges from the foramen perilymphaticum inferius to dilate into the saccus perilymphaticus, the modifications in these pipids are difficult to interpret. The direct continuity between the recessus partis basilaris and the intracranial perilymphatic space suggests that the latter, in *Hymenochirus* at least, is a combination of the parts defined by Harrison (1902) as spatium meningeale and saccus perilymphaticus. That such an arrangement is possible may be gathered from Harrison's conclusion that in the larva of *Bufo cinereus* the intracranial space is part of the saccus perilymphaticus and that there is no true spatium meningeale. Although de Burlet (1934) has obviated all con-

fusion arising from the vagaries in the derivation of the intracranial perilymphatic space by simply designating it the saccus perilymphaticus, it still seems advisable to differentiate between the two portions so carefully described by Harrison (1902). The spatium meningeale appears to be entirely intracranial and associated with the passage of the ductus perilymphaticus through the superior perilymphatic foramen, while the saccus perilymphaticus, although essentially an extracranial enlargement of the recessus partis basilaris, may,

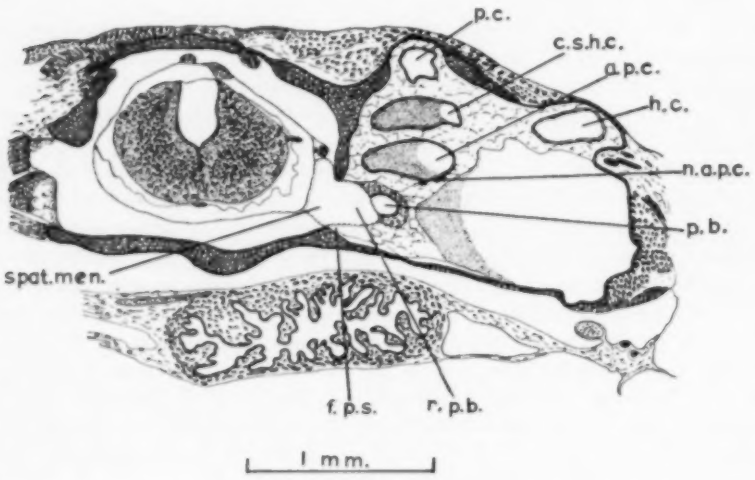


Fig. 11.—*Pipa pipa*. T. S. towards posterior end of inner ear showing pars basilaris separated from associated perilymphatic spaces by thin 'tympanal area'. (Key to lettering, p. 545.)

as in the larva of *Bufo*, be partly intracranial. While this interpretation has been applied to the parts in *Hymenochirus* (Fig. 12 C), it does not fully clarify the identity of the lower perilymphatic foramen in this animal, but, as there is no evidence of the foramen perilymphaticum inferius in its normal position in the floor of the auditory capsule, it may be assumed that, either it has combined with the foramen perilymphaticum accessorium at the beginning of the jugular foramen, or that it is entirely absent. The feasibility of the latter conclusion is manifest in the evidences of neoteny in the Pipidae, and in their ...ition of some of the anatomical features characteristic of Urodela. As Harrison (1902) has indicated, the foramen perilymphaticum inferius is absent in the Urodela, while in *Rana* it is a secondary elaboration associated with the posterior position of the recessus partis basilaris. It may well be that, in those Pipidae in which this recess and its expansion, the saccus perilymphaticus, are not markedly developed, the need for a foramen perilymphaticum inferius does not arise, for the same obscure reason as in the Urodela. At the same time, however, Harrison (1902) has observed that in larval stages of *Rana temporaria* and *Bufo cinereus* the recessus partis basilaris communicates with the cranial cavity through a single aperture, which represents a combination

of the superior and inferior perilymphatic foramina. It is thus equally possible that in *Hymenochirus* the foramen perilymphaticum inferius has been incorporated into the jugular foramen but, in the absence of information regarding the early development of the system, it is difficult to confirm this.

The other three species of Pipidae (Figs. 12 A, B, D) differ from *Hymenochirus* in that the ductus perilymphaticus is confined to the auditory capsule and, in this respect, the arrangement resembles that of Urodela and the larva of *Pelobates fuscus* investigated by Harrison (1902). Behind the recessus partis amphibiorum, the ductus continues directly to the recessus partis basilaris, which is ill defined in *Hemipipa*, but quite conspicuous in *Pipa* (r.p.b. Figs. 11, 12 B). In both species the characteristic ' tympanal area ' lies directly opposite the single perilymphatic foramen (f.p.s. Figs. 11, 12 A, B), through which the recessus is confluent with a relatively small intracranial perilymphatic space. It is difficult to determine if the latter is the spatium meningeale or the saccus perilymphaticus but, in view of the similarity to the urodele condition, it has been identified as the former (spat. men. Figs. 11, 12 A, B). As in *Hymenochirus*, there is again no indication of a true foramen perilymphaticum inferius opening extracranially from the auditory capsule and, but for the fact that the spatium meningeale accompanies the roots of cranial nerves IX and X for a short distance into the jugular foramen (f.jug. Figs. 12 A, B), the plan is almost identical with that of urodeles. In describing the skull of *Hemipipa* in 1955, the writer suggested that the single foramen might be comparable to the foramen perilymphaticum superius of other Anura, and the present observations tend to confirm this idea. In this connexion, it is of interest to note that in one-day-old larvae of *Hemipipa* the ductus perilymphaticus is not enlarged into recesses along its course, but passes directly through a single foramen to join the spatium meningeale. As the latter in turn extends into the jugular foramen, it is apparent that the condition in both larval and adult *Hemipipa* is essentially alike. This not only seems to support the conviction regarding the identity of the single perilymphatic foramen in *Pipa* and *Hemipipa*, but also indicates that, as in *Hymenochirus*, the inferior perilymphatic foramen is probably absent.

The relationships of the posterior parts of the perilymphatic system of *Xenopus* are also rather puzzling, as there appears to be a combination of features observed in other Pipidae with some that are characteristic of better known Anura. Some inconsistency was observed in the position of the connexion between intracranial and extracranial spaces, but this variability may be useful in reaching a better understanding of the homologies of the perilymphatic foramina in the family as a whole.

In all the metamorphosing and most of the postmetamorphic specimens of *Xenopus* examined there is no separate perilymphatic foramen in the medial wall of the auditory capsule. The conspicuous recessus partis basilaris lies in a posterior depression of the capsule and communicates through a ventral foramen with the saccus perilymphaticus. The latter (sac. per. Fig. 12 D) extends into the condyloid fossa, and is not only better defined than in the

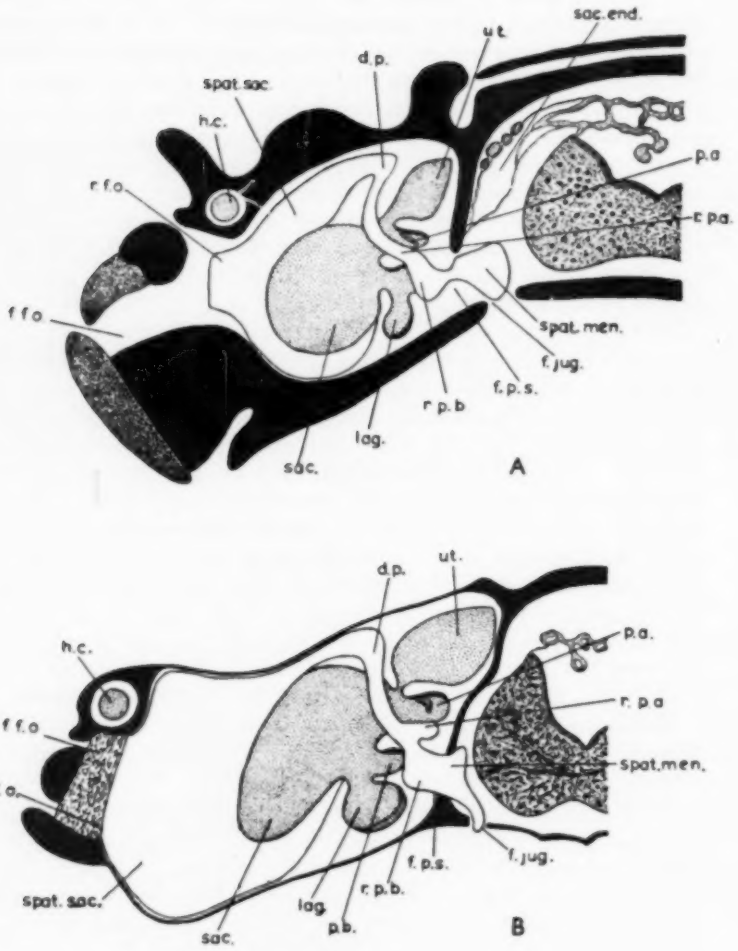
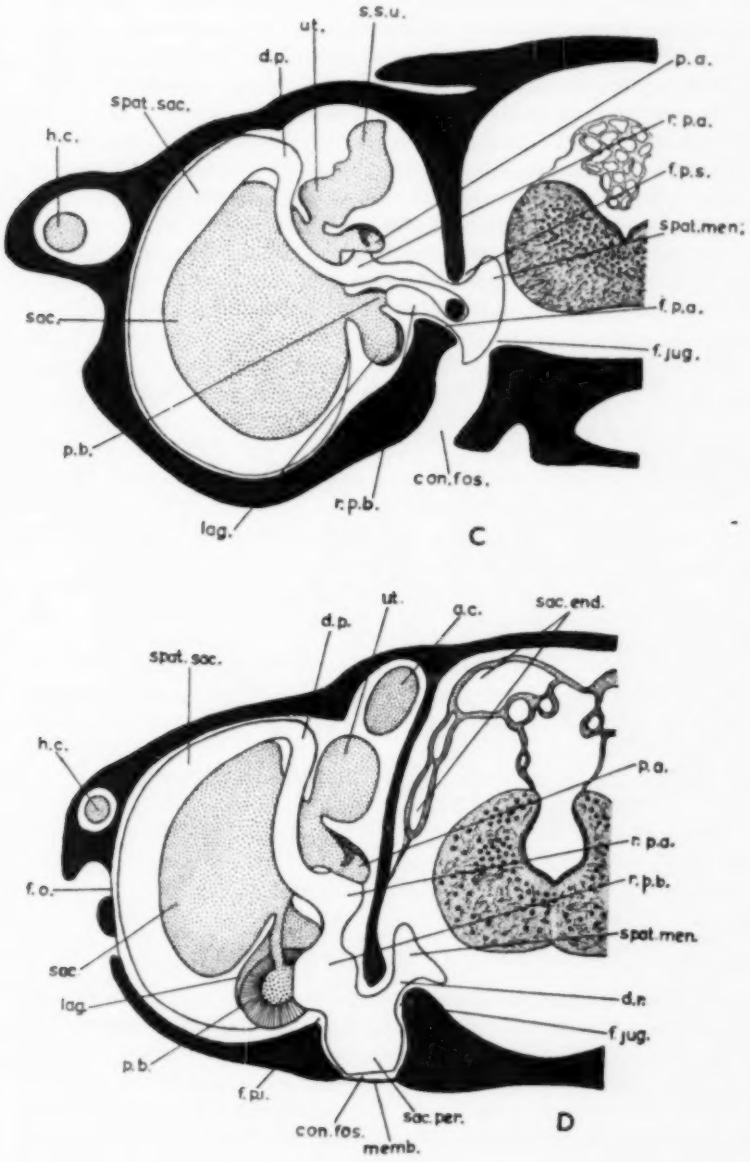


Fig. 12 A–D.—Diagramatic sections of inner ear, each compiled by the superposition of sections
Hemipipa is more lateral than is represented
12 A.—*Hemipipa carvalhoi*. × 15. 12 B.—*Pipa pipa*. × 30.



aken from different levels in the respective specimens. The foramen jugulare of *Pipa* and n the diagrams. (Key to lettering, p. 545.)

12 C.—*Hymenochirus curtipes*. × 30. 12 D.—*Xenopus laevis*. × 30.

other three species, but its passage (f.p.i.) from the auditory capsule is directly comparable to the foramen perilymphaticum inferius of *Rana*. In such specimens neither the ductus perilymphaticus nor the recessus partis basilaris establishes direct contact with any intracranial space but, at about the same level as the foramen perilymphaticum inferius, or sometimes slightly posterior to it, the saccus perilymphaticus has a dorsal diverticulum, which passes into the cranial cavity through the jugular foramen. It is thus evident that, of the four pipids studied, *Xenopus* alone provides distinct proof of the presence of a true inferior perilymphatic foramen in this family. Furthermore, as the arrangement broadly resembles that of the larva of *Pelobates fuscus* (Harrison, 1902), it is assumed that the intracranial space is the spatium meningeale (spat.men. Fig. 12 D) and that the superior perilymphatic foramen has merged with the jugular foramen and is no longer recognizable as a separate entity.

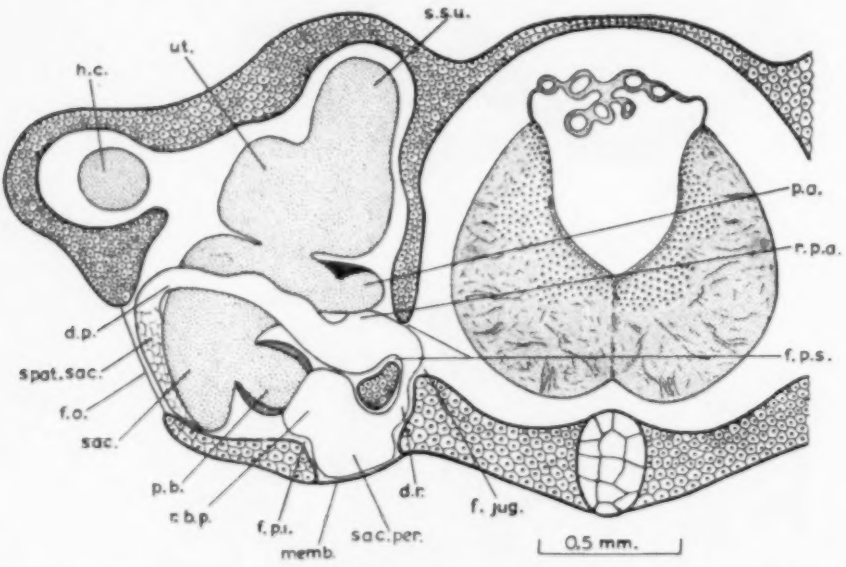


Fig. 13.—*Rana fuscigula*. Diagrammatic T. S. of inner ear of young larva ; total length 15 mm., comparable to Stage I of *Rana pipiens* (Taylor & Kollross, 1946). (Key to lettering, p. 545.)

Some confirmation of these conclusions seems to derive from observations on the perilymphatic system of *Rana fuscigula*, particularly in very young larvae, corresponding to Stage I in the developmental series of *Rana pipiens* (Taylor & Kollross, 1946) and approximating Stage 46 in the Normal Table of *Xenopus laevis* (Nieuwkoop & Faber, 1956). The main difference between the parts shown schematically in Fig. 13 and those of *Rana temporaria*, described and figured by Harrison (1902), is that there is no spatium meningeale in this early stage. The ductus perilymphaticus (d.p.) is easily traced through the foramen perilymphaticum superius (f.p.s.), and its continuation as the ductus reuniens (d.r.), passing through the anterior part of the jugular foramen,

links up with the recessus partis basilaris (r.p.b.) and the saccus perilymphaticus (sac.per.). A comparison of this diagram with that of *Xenopus* (Fig. 12 D) is also instructive as it indicates that, apart from the intracapsular course of the ductus perilymphaticus and the consequent absence of a discrete foramen perilymphaticum superius in *Xenopus*, the two systems are substantially alike.

As was previously indicated, in the majority of specimens of *Xenopus* (Fig. 12 D), the intracranial and extracranial perilymphatic spaces become united posteriorly after the saccus perilymphaticus has emerged from the auditory capsule into the condyloid fossa. In two postmetamorphic stages, however, the communication is effected rather more anteriorly through the antero-ventral part of the jugular foramen and just as the recessus partis basilaris is enlarging into the saccus perilymphaticus. Although there is virtually little difference between this arrangement and that observed in other specimens, the fact that the spaces may occasionally be connected at the anterior border of the jugular foramen corroborates the previous suggestion that the latter foramen and the foramen perilymphaticum superius have become confluent in *Xenopus*. The construction of the system in *Xenopus* also seems to support Harrison's conclusions (1902) regarding the secondary development of the foramen perilymphaticum inferius in Anura, for it is only in this pipid, where the pars basilaris is proportionally comparable to that of *Rana*, that this foramen is definitely established. In the other three pipids its apparent lack may be attributed to the relatively small, more anteriorly placed pars basilaris and its associated perilymphatic space.

CONCLUSIONS

While there is but little difference in the broad general outline of the inner ear in the four Pipidae which have formed the basis of the present observations, there are certain variations in anatomical detail that merit further consideration.

It seems feasible to assume that the presence of a single acoustic foramen in *Pipa* and *Hemipipa* is a neotenic feature, beyond which *Hymenochirus* and *Xenopus* have progressed by the acquisition of separate foramina for the passage of the anterior and posterior branches of the auditory nerve. The condition of the endolymphatic and perilymphatic systems also invites a similar interpretation, although there is evidence that both these systems are less specialized in *Hymenochirus* than in *Xenopus*. Further differentiation in the latter is the greater development of the pars basilaris, which is relatively small in the other three species, and is presumably morphologically and physiologically comparable to that of urodeles. As in the majority of amphibious Anura, the pars basilaris of *Xenopus* is a conspicuous part of the pars inferior of the labyrinth, and it is significant that associated with this there is a greater elaboration of the perilymphatic system.

The physiological implications of these structural variations in the Pipidae are rather obscure, but it is evident that on the whole the labyrinth of *Pipa*, *Hemipipa* and *Hymenochirus* shows little advance on the urodele condition, whereas that of *Xenopus* presents certain modifications which conform with the arrangement in other Anura. Although considerable progress has been

made in the localization of the equilibrial and vibrational receptors, some details of the physiology of the amphibian labyrinth are still imperfectly understood. Nothing definite is known concerning the function of the ' tympanal areas ' that feature in both Urodela and Anura. Dempster (1930) has suggested that they may allow of osmotic diffusion of fluid into the endolymphatic system, but Witschi, who refers to them as ' vestibular membranes ', considers that " they may be important barriers to chemical exchange between endolymph and perilymph " (1956, p. 176). He also does not associate them directly with sound transmission, but it is nevertheless conceivable that, as they appear to be placed at strategic points along the course of the ductus perilymphaticus, they may be of significance in the passage of sound and perhaps other oscillations to the sensoria with which they are intimately related. At the same time, it must be admitted that the precise function of some of the organs of the pars inferior is still conjectural and, consequently, the purpose of the ' tympanal areas ' remains equally uncertain.

From experimental work on fishes, von Frisch (1936, 1938) has concluded that the sensoria of the pars superior are concerned with the static function, while those of the pars inferior are auditory receptors. Similar functions have usually been attributed to the amphibian labyrinthine organs, but it is gradually becoming apparent that this broad generalization is no longer applicable to all fishes nor to the Anura that have been experimentally investigated. McNally & Tait (1925–26) have demonstrated that in the frog the semicircular canals are influenced by acceleration, the vertical canals being directly related to movements of the fore and hind limbs ; the utriculus was found to be the main organ showing gravity responses and, while the function of the sacculus was undetermined, it was definitely not involved in equilibration. The physiology of the frog's labyrinth has been further investigated by MacNaughton & McNally (1946), who have disclosed that, contrary to the opinions of earlier workers, the lagena is not an auditory receptor but is part of the equilibrial mechanism. The only organs for which no account has been given are the pars amphibiorum and the pars basilaris but, as MacNaughton & McNally (1946) have shown that they are not related with any gravity responses, it may be assumed that they are vibration receptors. It is of interest to note that most of these conclusions have been substantiated by the more recent experiments of Lowenstein & Roberts (1948, '50, '51) on the labyrinth of *Raja clavata*. By electro-physical means they have analyzed the oscillations from the nerves supplying the individual sensory areas and, among other things, have discovered that a small portion of the recessus utriculi, the lacinia, and also the macula neglecta, which they associate with the sacculus, are highly sensitive to vibrational stimuli. As de Burlet (1934) and others have maintained that the macula neglecta has no true homologue in the amphibian labyrinth, the previously used term, pars neglecta, has been abandoned in favour of the pars amphibiorum. If, however, the facts revealed by Lowenstein & Roberts can be applied to the amphibian labyrinth, it seems likely that the papilla amphibiorum is at least functionally similar to the elasmobranch macula neglecta, and may therefore be an important vibrational centre.

The pars amphibiorum and the pars basilaris are distinctive features of the amphibian inner ear and, in the absence of experimental proof, it may be assumed that they could contribute towards a better discrimination of sound, but there is also a possibility that they differ functionally from each other. Some suggestion of this is indicated in the Pipidae by the fact that, quite apart from the ' tympanal area ', there is another appreciable thinning of the antero-lateral wall of the pars basilaris, directly opposite the papilla basilaris. The latter is, therefore, in a position to receive impulses from both the spatium sacculare and the recessus partis basilaris, while the papilla amphibiorum is presumably only stimulated via the ductus perilymphaticus. From other considerations of the auditory region of Anura, Eiselt (1941) has also concluded that the papilla amphibiorum and the papilla basilaris are capable of responding to different types of stimuli and has suggested that, whereas the former may be sensitive to single, strong impulses, the latter probably reacts to repeated sound and mechanical vibrations.

It also seems highly probable that in *Xenopus*, as in some of the Anura investigated by Harrison (1902), the pars basilaris is of greater physiological importance than in other Pipidae, and that the direct result of this has been the development of the foramen perilymphaticum inferius. Through this aperture the perilymphatic system acquires an extracranial outlet from the auditory capsule, while in the other three species it is projected into the cranial cavity. In either arrangement the terminal space must act as a relief mechanism for pressure variations within the labyrinth and perhaps also for fluctuations in intracranial tension. Somewhat similar conclusions have been reached by Tumarkin (1948 c), who argues that a greater efficiency in the sound transmitting apparatus is inherent in the presence of an extracranial perilymphatic foramen and its membrane, the ' round window '. The obvious deduction from this would be that, among Pipidae, *Xenopus* is the best equipped for ' hearing ', but the reason for this adjustment in only one member of a family of essentially aquatic animals is not apparent. It is certainly another instance of the variation and specialization found in nearly every system of organs in this pipid. Noble's comparative studies of the musculature and skeletal anatomy of Anura (1922) have revealed similar interesting anomalies in this genus, and it has been assumed by the writer (1949) that they signify the retention of some of the characteristics of semi-terrestrial ancestors by forms which have secondarily become adapted for an aquatic mode of life. Based on an analysis of the vascular system of *Leiopelma* relative to that of *Bombina* and *Xenopus*, Szarski (1951) has expressed similar opinions regarding the Pipidae, while Eiselt (1941) has estimated that the absence of the operculum and the musculus opercularis is an indication of an ancient, secondary adaptation to the aquatic habit. There is little doubt that all the Pipidae present distinct evidences of neoteny and these are correlated with their habits. In *Xenopus*, however, superimposed on the neotenic features are a number of striking peculiarities, some of which are not altogether compatible with the findings in other aquatic forms. Although these tend to obscure its affinities, they give the impression that *Xenopus* is more nearly

related to the true frogs and toads than is any other representative of the family.

It may seem that undue importance has been attached to the differences observed in the inner ear of Pipidae, and especially to those concerning the perilymphatic system, but they seem to be pertinent to an inquiry into Witschi's recent pronouncements (1947–56) regarding the presence of accessory auditory structures in larvae of Ranidae and *Xenopus laevis*. As previously noted, the perilymphatic system of *Xenopus* resembles that of *Rana* in having a conspicuous terminal saccus perilymphaticus which leaves the auditory capsule through the inferior perilymphatic foramen. Harrison's expression of doubt (1902) as to the homology of this foramen with the fenestra rotunda of other vertebrates seems justifiable in that it does not open directly through the floor of the auditory capsule but communicates with the condyloid fossa. It is obvious, however, that the elastic membrane (memb. Figs. 12 D, 13), which spans the condyloid fossa and adjoins the saccus perilymphaticus, must be functionally similar to the 'round window' and must vibrate in phase with impulses received at the fenestra ovalis.

In premetamorphic larvae of *Xenopus* a pair of dorsal outgrowths (br.div. Fig. 1) near the posterior end of the bronchus bulge forward into the anterior part of the coelom and become approximated to the posterior walls of the sacci perilymphatici. Fibrous tissue connected with the lateral base of each diverticulum appears to be associated with the aponeurosis attaching the musculi dilator laryngis and levator arcuum branchialium iv to the muscular process of the auditory capsule (mus. proc.). It is in no way related to the saccus perilymphaticus, but merely seems to act as a bronchial suspension, passing through which is the pulmonary nerve to the lateral wall of the lung. Associated with it, however, and immediately in front of the bronchial diverticulum is another fibrous band (sep. Fig. 1), some of the fibres of which approach the base of the condyloid fossa and resemble the fibrous structures described by Harrison (1902) and Witschi (1947–56) in larvae of *Rana*. It passes horizontally between the oesophagus and the bronchus and, as it is apparent before and after the development of the bronchial diverticula, it seems to be comparable to the septum arcuatum dorsale underlying the perioesophageal lymph space in *Rana* (Gaupp, 1904).

At certain stages prior to and during early metamorphosis in different species of *Rana*, Witschi (1947–56) has observed a strong fibrous cord, the 'bronchial columella', which embraces a 'bronchial membrane' or diverticulum and connects the bronchus with the 'round window'. These findings are substantially similar to those of Harrison (1902), who associated the dense fibrous strand in larvae of *Rana temporaria* and *Pelobates fuscus* with their aquatic life and interpreted it as a means of transmitting variations in hydrostatic pressure from the lung to the ear. Witschi's observations however, differ from those of Harrison in that the 'bronchial columella' of *Rana catesbeiana* and other species is a solid ("partially cartilaginous", 1947) rod, which for a period is engulfed by the dorsal aorta. He makes the ingenious suggestion (p. 239, 1949; p. 176, 1956) that "in frog larvae the

lungs serve as ear drums ", and that the conduction of sound vibrations from the lungs to the ' round window ' is freed from local interference by the passage of the ' bronchial columella ' through the aorta.

Harrison's (1902) study of *Rana temporaria* and an examination of sections of *R. fuscigula* larvae suggest that a ' bronchial columella ' traversing the aorta is not applicable to all species of *Rana* as Witschi (1955) has concluded. Witschi attributes Harrison's failure to observe a ' bronchial columella ' in the aorta to the fact that conclusions were based on an examination of a metamorphosing specimen, but it is clear from Harrison's description that the structural arrangement was traced through various developmental stages. In *R. fuscigula* (Fig. 14) the bronchial diverticula (br. div.) are highly vascular

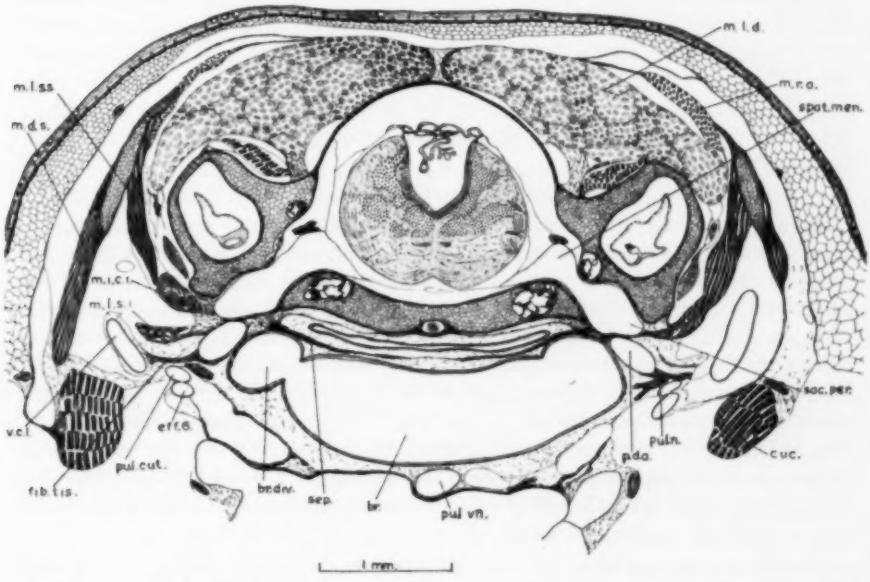


Fig. 14.—*Rana fuscigula*. T. S. through posterior region of auditory capsule, immediately posterior to ductus Botalli, during early metamorphosis. Total length of larva 52 mm., comparable to Stage XXI of *Rana pipiens* (Taylor & Kollrose, 1946). The section has been chosen to show the relationship between the sacci perilymphatici and the bronchial diverticula. (Key to lettering, p. 545.)

and seem to be rather more closely approximated to the sacci perilymphatici (sac.per.) than in other species. As in *Xenopus* larvae, fibrous tissue (fib.tis. Fig. 14) attached to the wall of the bronchus appears to be associated with the strong tendinous aponeurosis of the branchial and dilatator laryngeal muscles. Together with the pulmonary nerve (pul.n.) it passes beneath the paired dorsal aorta (p.d.a.) close to the junction of the latter and the ductus Botalli, which persists for a longer period than in *Xenopus*. Medial to the paired dorsal aorta, the space between the bronchial diverticulum and the saccus perilymphaticus is filled with connective tissue, which becomes densely fibrous in part

and is evidently comparable to the fibrous strand described by Harrison (1902) and the ' bronchial columella ' reported by Witschi (1947–56) in other species of *Rana*. Careful scrutiny of the sections, however, does not reveal any trace of it in the lumen of the paired dorsal aorta. The denser part of the strand (sep. Fig. 14), composed of tissue resembling unstriped muscle fibres, stretches medially over the dorsal wall of the bronchus to become continuous with its counterpart on the opposite side. Harrison (1902) has described a similar arrangement in larvae of *Pelobates fuscus* and, although Witschi (1955) doubts the occurrence of such a structure in this species, it seems highly probable that in both *Pelobates* and *Rana* it represents part of the septum separating the perioesophageal lymph sinus from the bronchus. It is thus of interest to observe that, although the bronchial diverticula of *R. fuscigula* are stouter and more vascular than those of *Xenopus laevis* (Fig. 1), there is some resemblance in the arrangement of the parts in the two species. It is considered that in neither of them is there a ' bronchial columella ' as defined by Witschi, but this does not preclude the possible transmission of vibrations between the bronchial diverticula and the sacci perilymphatici at their point of approximation.

While a different interpretation is herein ascribed to the fibrous strand lying dorsal to the bronchus, there is much that is novel and interesting in Witschi's thesis (1947–56) concerning the function of the bronchial structures in *Rana* and *Xenopus*. His views (1955) are based on the examination of the condition in a number of larvae belonging to different families, but it is felt that, as yet, the anatomical and physiological details are insufficiently understood to substantialize the claim that they participate in sound conduction. The enclosure of the ' bronchial columella ' by the aorta is also remarkable, and it is questionable if its passage through the blood vessel would result in the advantages suggested by Witschi. It seems more likely that, being bathed in blood under pressure from the ventricle, it would be subjected to forces that would tend to deflect any impulses conducted by it away from and not towards the auditory capsule.

As far as is known, in anuran larvae there are no muscle connexions between the auditory capsule and other skeletal elements capable of functioning in the transmission to the ear of stimuli received at the surface. In any case, the purpose of such connexions in adult frogs is still in dispute, and Eiselt (1941) has concluded from observations on the middle ear of a large number of Anura that, contrary to previous concepts, the opercular apparatus does not serve to conduct vibrations, but is a " Bewegungskorrelation " occurring more especially in terrestrial forms. The lateral-line organs, however, which are retained by adult Pipidae, constitute an important sensory apparatus for the perception of pressure variations in the surrounding medium, associated with which the lungs are also of some consequence. In young specimens of *Pipa* removed from the incubatory pouches on the back of the parent, the ear (Figs. 2, 6, 8, 9, 11) is completely formed, but the lungs are less capacious and more posterior in position than in the free-swimming larvae of *Xenopus* and *Rana*. The relative diminution of the lungs in the early stages of *Pipa* thus

appears to be consistent with the belief expressed by Noble (1931) that, in the aquatic larvae and adults of Pipidae, the lungs are important hydrostatic organs. The development of bronchial outgrowths in larval *Xenopus* may be contributory to such a process, but in this species it is also possible that they are simply incidental to premetamorphic changes taking place in the coelom and various organs in the neighbourhood of the pharynx. If some special functional significance attaches to them, it is remarkable that they do not persist into the adult state, in which the body is subjected to similar environmental conditions. Furthermore, the position of these so-called bronchial diverticula in larval *Xenopus laevis* and *Rana fuscigula* and their more obvious vascularity in the latter species suggest that, instead of being actual bronchial structures, they are merely temporary, dorso-lateral projections of the lungs, with the respiratory and hydrostatic functions of which they may be related.

As 'hearing' may be considered to be a specialized or refined form of pressure reception, the possible contribution of the lateral-line system of Pipidae to sound reception cannot be overlooked, but the subtle discrimination of stimuli must be localized in the sensory areas of the labyrinth. Witschi, Bruner & van Bergeijk (1953 a) have concluded that the ear of adult *Xenopus* is perfectly adapted for the reception of sound waves skimming over the surface of the water and, from results of experiments with a hydrophone (1953 b), have suggested that the sounds produced by the males indicate that the ear would be sensitive to a frequency of approximately 1,500 cycles per second. Other available literature reveals that in Anura the semi-circular canals, the utriculus and the lagena are concerned with the maintenance of balance and, although the function of the pars amphibiorum and the pars basilaris is still undetermined, it is highly probable that they act as auditory receptors. MacNaughton & McNally (1946) have found that the sacculus of *Rana* is not associated with the static function, but the presence of a definite otolith and the double innervation of its macula in some Pipidae suggest its potentiality for participation in gravitational as well as vibrational responses. While it is conceded that the evidence for 'hearing' in larval and adult Pipidae is rather tenuous and still a matter for conjecture, it is considered that the study of the structure of the ear forms a basis which justifies the assumption that the parts perform functions similar to those that have been experimentally demonstrated in other frogs by McNally & Tait (1925–26) and MacNaughton & McNally (1946). In all essential details the labyrinth of Pipidae, and especially that of *Xenopus*, is equivalent to that of *Rana*, and its various sensoria seem to be equally important as selective areas for the reception of different kinds of stimuli.

ACKNOWLEDGMENTS

The writer would like to express her indebtedness to Professors C. G. S. de Villiers and C. A. du Toit, of the University of Stellenbosch, for the use of their serial sections of the head of the adult *Hymenochirus curtipes* and also for supplying the adult specimen of *Hemipipa carvalhoi*. Grateful acknowledgments are also due to Dr A. L. de Carvalho, of the Museu Nacional, Rio de

Janeiro, who kindly forwarded several specimens of one-day-old larvae of *Hemipipa carvalhoi*. The material for two series of sections of juvenile *Pipa pipa*, obtained some time ago from Professor C. J. van der Horst, of the University of the Witwatersrand, was compared with a similar series prepared in the Department of Zoology, University of Stellenbosch. Dr N. A. H. Millard's excellent sections of various stages of *Xenopus laevis* have also proved to be an invaluable adjunct to preparations of this species previously microtomised and studied by the writer.

SUMMARY

Based on serial sections of heads of *Pipa pipa*, *Hemipipa carvalhoi*, *Hymenochirus curtipes* and *Xenopus laevis*, a comparative study of the component parts of the labyrinth indicates that in the Pipidae the structural plan is fairly consistent and that the variations are evidences of different degrees of neoteny.

From observations on the endolymphatic and perilymphatic systems it is considered that the inner ear of *Xenopus* is more specialized than that of the other three species.

Correlated with the better development of the pars basilaris in *Xenopus* is the presence of a foramen perilymphaticum inferius, which is not apparent in the other specimens.

The structural details of the labyrinth of *Xenopus* are compatible with those of other Anura, while in the other three Pipidae there is a closer resemblance to the arrangement in the Urodela.

It seems reasonable to assume that the functional features, which have been demonstrated experimentally in the labyrinth of *Rana* by various investigators, are also applicable to the labyrinthine sensory areas of the Pipidae.

An examination of sections of larvae of *Rana fuscigula* reveals that, although the saccular nerve is a ramulus of the anterior branch of the auditory nerve, its fibres are derived mainly from the postero-dorsal root of VIII.

It has been concluded that the structure described by Harrison (1902) as a fibrous strand and by Witschi (1947–56) as the bronchial columella in larvae of *Rana* may be part of the septum separating the bronchus from the perioesophageal lymph sinus, and that there is a similar arrangement in *Xenopus* larvae.

It is thought that the so-called bronchial diverticula or bronchial membranes in larvae of *Xenopus* and *Rana* are antero-dorsal evaginations of the lungs and that, as yet, there is insufficient evidence to determine if they are auditory in function. It is possible that they are concerned with the hydrostatic function, and that the lateral-line organs are potential auditory receptors.

ADDENDUM

Since the above was written, I. I. Schmalhausen's article on "The origin of the Amphibia", published in the Proceedings of the XVth International Congress of Zoology, London, 1959, pp. 455–458, has come to hand.

In it are some interesting remarks concerning the ear of Amphibia. It is

not only indicated that in the development of Hynobiidae there is proof that the hyomandibula is transformed into part of the sound transmitting apparatus, but it is also suggested that in aquatic forms the cutaneous veins of the head may be instrumental in conducting sounds towards the endolymphatic system and so to the macula neglecta amphibiorum. The opinion is also expressed that sound conduction from the ground to the ear via the fore limb is a physiological impossibility, and that the operculum " is not an ear bone, it is a mechanism reducing pressure in the perilymph and protecting the receptors from shakings ".

REFERENCES

Adrian, E. D., Craik, K. J. W. & Sturdy, R. S. (1938). The electrical response of the auditory mechanism in cold-blooded vertebrates. *Proc. roy. Soc. Lond.* (B) **125** : 435–455.

Cordier, R. & Dalcq, A. (1954). Organe Stato-acustique—in Grassé's *Traité de Zoologie* **12** : 453–521.

De Beer, G. R. (1937). *The development of the vertebrate skull.* Oxford : Clarendon Press.

De Burlet, M. M. (1934). Vergleichende Anatomie des stato-akustischen Organs-in Bolk, Göppert, Kallius und Lubosch : *Handb. vergl. Anat. Wirbelt.* **2** : 2. Berlin.

De Carvalho, A. L. (1939). Notas sôbre *Hemipipa carvalhoi* Mir.-Rib. (Batrachia, Anura : Pipidae). *Bol. Biol.* (N.S.) **4** No. 3 : 394–414.

Dempster, W. T. (1930). The morphology of the amphibian endolymphatic organ. *J. Morph.* **50** : 71–126.

De Villiers, C. G. S. (1931). Some features of the cranial anatomy of *Hemisus marmoratus*. *Anat. Anz.* **71** : 305–331.

De Villiers, C. G. S. (1932). Über das Gehörskelett der Aglossen Anuren. *Ibid.* **74** : 33–55.

De Villiers, C. G. S. (1934). Studies of the cranial anatomy of *Ascaphus truei* Stejneger, the American liopelmid. *Bull. Mus. comp. Zool. Harv.* **77** : 1–38.

Dunn, E. R. (1948). American frogs of the family Pipidae. *Amer. Mus. Novit.* No. 1384 : 1–13.

Eiselt, J. (1941). Der Musculus opercularis und die mittlere Ohrsphäre der anuren Amphibien. *Arch. Naturg.* N. F. **10** 2 : 179–230.

Ferhat-Akat, S. (1939). Untersuchungen über den Gehörsinn der Amphibien. *Z. vergl. Physiol.* **26** : 253–281.

Gaupp, E. (1896–1904). A. Ecker's und R. Wiedersheim's '*Anatomie des Frosches*', **1–3**, Braunschweig.

Gazagnaire, C. (1932). Origine de l'oreille moyenne chez *Rana temporaria*. *C. R. Soc. Biol., Paris* **110** : 1076–1078.

Greene, W. F. & Laurens, H. (1923). The effect of extirpation of the embryonic ear and eye on equilibration in *Amblystoma punctatum*. *Amer. J. Phys.* **64** : 120–143.

Gruenberg, B. C. (1907). Compensatory motions and the semi-circular canals. *J. exp. Zool.* **4** : 447–467.

Harrison, H. S. (1902). On the perilymphatic system of the amphibian ear. *Int. Mechr. Anat. Physiol.* **19** : 221–261.

Herter, K. (1921). Untersuchungen über die nicht-akustischen Labyrinthfunktionen bei Anurenlarven. *Z. allg. Physiol.* **19** : 335–414.

Hilton, W. A. (1952). The ear components of salamanders. *Trans. Amer. micr. Sci.* **71** : 405–408.

Johnson, M. L. (1952). Herpetological notes from North-Eastern Brazil. *Copeia* **1952** : 283–284.

Jones, F. R. H. & Marshall, N. B. (1953). The structure and functions of the teleostean swimbladder. *Biol. Rev.* **28** : 16–83.

Kramer, G. (1932/33). Untersuchungen über die Sinnesleistungen und das Orientierungsverhalten von *Xenopus laevis*. *Zool. Jahrb.* (Zool.) **52** : 629–676.

Lowenstein, O. (1936). The equilibrium function of the vertebrate labyrinth. *Biol. Rev.* **11** : 113–145.

LOWENSTEIN, O. & ROBERTS, T. D. M. (1948). Oscillographic analysis of the gravity and vibration responses from the labyrinth of the thornback ray (*Raja clavata*). *Nature, Lond.* **162** : 852.

LOWENSTEIN, O. & ROBERTS, T. D. M. (1950). The equilibrium function of the otolith organs of the thornback ray (*Raja clavata*). *J. Physiol.* **110** : 392–415.

LOWENSTEIN, O. & ROBERTS, T. D. M. (1951). The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in vertebrates. *Ibid.* **114** : 471–489.

MCNALLY, W. J. & TAIT, J. (1925–26). Ablation experiments on the labyrinth of the frog. *Amer. J. Phys.* **75** : 155–179.

MACNAUGHTON, I. P. J. & MCNALLY, W. J. (1946). Some experiments which indicate that the frog's lagena has an equilibrial function. *J. Laryng. Otol.* **61** : 204–214.

NIEUWKOOP, P. W. & FABER, J. (1956). *Normal table of* Xenopus laevis. Amsterdam.

NOBLE, G. K. (1922). The phylogeny of the Salientia. I. The osteology and thigh musculature ; their bearing on classification and phylogeny. *Bull. Amer. Mus. nat. Hist.* **46** : 1—87.

NOBLE, G. K. (1931). *The biology of the Amphibia.* New York.

NORRIS, H. W. (1913). The cranial nerves of *Siren lacertina*. *J. Morph.* **24** : 245–338.

PATERSON, N. F. (1949). The development of the inner ear of *Xenopus laevis*. *Proc. zool. Soc. Lond.* **119** : 269–291.

PATERSON, N. F. (1955). The skull of the toad, *Hemipipa carvalhoi* Mir.–Rib., with remarks on other Pipidae. *Ibid.* **125** : 223–252.

PEARSON, A. A. (1936). The acustico-lateral nervous system in fishes. *J. comp. Neur.* **64** : 235–273.

PROSSER, C. L. et al. (1952). *Comparative animal physiology.* Philadelphia.

PUMPHREY, R. J. (1950). Hearing. *Symp. Soc. exp. Biol.* **4** : 3–18.

REED, H. D. (1920). The morphology of the sound-transmitting apparatus in caudate Amphibia and its physiological significance. *J. Morph.* **33** : 325–387.

SAND, A (1937). The mechanism of the lateral line sense organs of fishes. *Proc. roy. Soc. Lond.* **123** : 472–495.

SLABBERT, G. K. (1945). Contributions to the cranial morphology of the European anuran, *Bombina variegata* (Linné). *Ann. Univ. Stellenbosch*, **23** Sect. A, No. 5 : 67–89.

SLABBERT, G. K. & MAREE, W. A. (1945). The cranial morphology of the Discoglossidae and its bearing upon the phylogeny of the primitive Anura. *Ibid.* **23** Sect. A, No. 6 : 91–97.

STEPHENSON, N. G. (1951). On the development of the chondrocranium and visceral arches of *Leiopelma archeyi*. *Trans. zool. Soc. Lond.* **27** : 203–253.

STEPHENSON, E. M. (1951). The anatomy of the head of the New Zealand frog, *Leiopelma*. *Ibid.* **27** : 255–305.

SZARSKI, H. (1951). Remarks on the blood-vascular system of the frog *Leiopelma hochstetteri* Fitzinger. *Trans. roy. Soc. N. Z.* **79** : 140–147.

TAYLOR, A. C. & KOLLROSS, J. J. (1946). Stages in the normal development of *Rana pipiens* larvae. *Anat. Rec.* **94** : 7–23.

TUMARKIN, A (1948 a). The evolution of the auditory conducting apparatus. A new synthesis based on functional considerations. *Proc. R. Soc. Med.* **41** : 877–888.

TUMARKIN, A. (1948 b). On the phylogeny of the mammalian ossicles. *J. Laryng. Otol.* **62** : 687–690.

TUMARKIN, A. (1948 c). On the evolution of the auditory perilymphatic system. *Ibid.* **62** : 691–701.

VAN DER HORST, C. J. (1934). The lateral-line nerves of *Xenopus*. *Psychiat. Neurol. Bl. Amst.* No. 3 & 4 : 426–435.

VON FRISCH, K. (1936). Über den Gehörsinn der Fische. *Biol. Rev.* **11** : 210–246.

VON FRISCH, K. (1938). The sense of hearing in fish. *Nature, Lond.* **141** : 8–11.

WAGNER, D. S. (1934/35). The structure of the inner ear in relation to the reduction of the middle ear in the Liopelmidae (Noble). *Anat. Anz.* **79** : 20–36.

WEISZ, P. (1945). The development and morphology of the larva of the South African clawed toad, *Xenopus laevis*. *J. Morph.* **77** : 163–192.

WESTOLL, T. S. (1943). The hyomandibular of *Eusthenopteron* and the tetrapod middle ear. *Proc. roy. Soc. Lond.* (B) **131** : 393–414.

WHITESIDE, B. (1922). The development of the saccus endolymphaticus in *Rana temporaria* Linné. *Amer. J. Anat.* **30** : 231–266.

WITSCHI, E. (1947). Development and metamorphosis of the auxiliary apparatus of the ear of the frog. *Anat. Rec.* **99** Abstr. 21 : 568.

WITSCHI, E. (1949). The larval ear of the frog and its transformation during metamorphosis. *Z. Naturforsh.* **4** : 230–242.

WITSCHI, E. (1950). The bronchial diverticula of *Xenopus laevis* Daudin. *Anat. Rec.* **108** No. 3, Abstr. 169 : 590.

WITSCHI, E. (1955). The bronchial columella of the ear of larval Ranidae. *J. Morph.* **96** : 497–511.

WITSCHI, E. (1956). *Development of vertebrates*. Philadelphia.

WITSCHI, E., BRUNER, J. A. & VAN BERGEIJK, W. A. (1953 a). The ear of the adult *Xenopus*. *Anat. Rec.* **117** Abstr. 161 : 602–603.

WITSCHI, E., BRUNER, J. A. & VAN BERGEIJK, W. A. (1953 b). Sound production by *Xenopus*. *Ibid.* **117** Abstr. 229 : 636.

KEY TO THE LETTERING TO FIGURES

a.a.c.	ampulla of anterior canal.
a.c.	anterior vertical semicircular canal.
acus.	acoustic ganglion.
a.h.c.	ampulla of horizontal canal.
ant.coel.	anterior part of coelom.
a.p.c.	ampulla of posterior canal.
a.tym.	annulus tympanicus.
br.	bronchus.
br.div.	bronchial diverticulum.
con.fos.	condyloid fossa.
constr.	m. constrictor branchialis.
c.s.h.c.	crus simplex canalis horizontalis.
cuc.	m. cucullaris.
d.C.	ductus Cuvieri.
d.e.	ductus endolymphaticus.
dien.	diencephalon.
dil.lar.	m. dilatator laryngis.
d.p.	ductus perilymphaticus.
d.r.	ductus reuniens.
eff.6	sixth efferent branchial vessel.
Eus.	Eustachian tube.
f.end.	foramen endolymphaticum.
f.f.o.	fossa fenestrae ovalis.
fib.tis.	fibrous tissue.
f.jug.	foramen jugulare.
f.o.	fenestra ovalis.
f.p.a.	foramen perilymphaticum accessorium.
f.p.i.	foramen perilymphaticum inferius
f.p.s.	foramen perilymphaticum superius.
f.u.s.	foramen utriculo-sacculare.
h.c.	horizontal semicircular canal.
hyp.	hypophysis.
jug.gn.	jugular ganglion.
lag.	lagena.
lev.	m. levator arcuum branchialium iv.
m.d.s.	m. dorsalis scapulae.
memb.	elastic membrane at condyloid fossa.
m.i.c.i.	m. intertransversarius capitis inferior.
m.lag.	macula lagenae.
m.l.d.	m. longissimus dorsi.
m.l.s.i.	m. levator scapulae inferior.
m.l.s.s.	m. levator scapulae superior.
m.r.a.	m. rhomboideus anterior.
m.sac.	macula sacculi.
mus.proc.	muscular process of auditory capsule.
m.ut.	macula utriculi.
n.a.a.c.	ramulus ampullae anterioris.
n.a.h.c.	ramulus ampullae horizontalis.
n.a.p.c.	ramulus ampullae posterioris.
n.lag.	ramulus lagenae.
n.p.a.	ramulus partis amphibiorum.
n.p.b.	ramulus partis basilaris.
n.sac.	ramulus sacculi.
p.a.	pars amphibiorum.
p.b.	pars basilaris.
p.c.	posterior vertical semicircular canal.
p.d.a.	paired dorsal aorta.
pul.cut.	pulmo-cutaneous arch.
pul.n.	pulmonary nerve.
pul.vn.	pulmonary vein.
r.f.o.	recessus fenestrae ovalis.
r.l.a.	ramus lateralis anterior.

r.p.a.	recessus partis amphibiorum.
r.p.b.	recessus partis basilaris.
r.ut.	recessus utriculi.
sac.	sacculus.
sac.end.	saccus endolymphaticus.
sac.per.	saccus perilymphaticus.
sep.	possible septum arcuatum dorsale.
spat.men.	spatium meningeale.
spat.sac.	spatium sacculare.
s.p.u.	sinus posterior utriculi.
s.s.u.	sinus superior utriculi.
trans.	m. transversus ventralis iv.
ut.	utriculus.
v.c.l.	vena capitis lateralis.
V, VII, VIII.	cranial nerves.

SEASONAL CHANGES IN THE MALLARD'S PENIS AND THEIR HORMONAL CONTROL

BY

E. O. HÖHN, M.B., B.S., Ph.D.

Department of Physiology, University of Alberta, Edmonton, Alberta, Canada

[Accepted 10th November, 1959]

(With 1 figure in the text)

In adult wild mallards the penis weighs about 0·6 gms (0·05 per cent of body weight) for most of the year but increases to a weight of almost 3 gms. (0·3 per cent of body weight) at the height of the breeding season. In immature birds which had reached adult body weight the average penis weight was only 0·03 gms. (0·0026 per cent of body weight). The breeding season penile enlargement could be prevented by castration early in the spring. Evidence that Testosterone administration can cause enlargement of the penis in adult mallards was also obtained. Unilateral adrenalectomy did not effect penile or testicular weight.

CONTENTS

	Page
Introduction	547
Materials and methods	548
Results and discussion	550
1. Seasonal chances in weight of testes and penis of adult mallards	550
2. The effect of complete and partial castration on penis weight in adult mallards	551
3. The effect of Testosterone administration on penis weight in adult mallards	552
Acknowledgments	555
References	555

INTRODUCTION

The anserines are one of the few groups of birds in which a male copulatory organ is found. In birds the penis is generally regarded as a primitive character. Its retention in anserine birds may be related to their habit of copulating on water, with the caudal parts of the body of both partners becoming submerged during the sex act. Grebes and divers, though otherwise almost exclusively aquatic in mode of life, apparently copulate out of water on their nests or on shore (Witherby *et al.* 1943).

The hormonal control of the avian penis has not been studied extensively. Champy *et al.* (1932) found that castration of male domestic ducklings (of unstated breed) caused the penis to retain its small prepuberal size but that castration in adults produced no noticeable reduction in size of this organ. Bénoit in Grassé (1950) showed that artificial lighting of immature male domestic ducks of the Rouen breed produced testicular enlargement together with an enlargement of the penis. Wolff & Wolff (1948) have shown that

in the embryos of ducks of this breed, the rudimentary penis develops equally in both sexes for the first two weeks of incubation and that its further development thereafter in female embryos is inhibited by oestrogen. They also showed that in males the subsequent embryonic development is not androgen dependent. The later puberal development of the penis in males at 6–8 months of age does however follow testicular maturation closely and since, as shown by Champy *et al.* (1932), it can be prevented by prepuberal castration, maturation of the avian penis like that of other accessory male sex organs appears to be androgen controlled. The results reported below indicate that in wild mallard ducks (*Anas platyrhyncha* (L.)), which, unlike domestic ducks, have a restricted annual breeding season, a seasonal enlargement of the penis occurs during the breeding season. Castration in the early spring could prevent the breeding season penile enlargement and some evidence that testosterone administration before the breeding season can cause penile enlargement is also presented.

MATERIALS AND METHODS

For the observations on seasonal trends in penis size twenty-eight adult male mallards and nine juvenile males were shot in the course of several years in the Edmonton district of Alberta. Since mallards leave most of this area for the winter some birds were also obtained from a wintering flock at Calgary, Alberta and these were kept for some weeks after capture in the Edmonton Zoo before being killed and examined. Birds thus kept captive before examination are indicated in Table 1 by the letter " Z ". As can be seen from Table 1, in those cases in which birds shot in the wild and others first kept in captivity were killed at about the same period, the sex cycle seems to be much the same in the two groups.

The dead birds were weighed and the plumage was examined. The testes and penis were then removed by dissection and kept in 10 per cent formol saline. After overnight fixation excess moisture was removed from these tissues which were then weighed. Paraffin sections were made from the testes and stained with haematoxylin eosin, to determine whether spermatogenesis had occurred in any particular case. The penis was merely weighed after fixation.

Castrations were performed under chloroform-ether anaesthesia. The birds were then killed four, and in some cases six weeks after the operation and examined as above. A number of castrations were found to have been incomplete and are recorded separately in Table 2. " Complete castrations " are only those cases in which macroscopic post mortem examination failed to show any testicular tissue or those in which possible regenerated testicular tissue (sometimes displaced within the abdomen) was shown by microscopic examination not to contain testicular elements. Controls were subjected to a sham operation in which the testes were merely exposed under anaesthesia and the abdominal wounds were then closed, four to six weeks before the birds were killed and examined.

Testosterone administration was carried out on two birds (marked with an asterisk in Table 3) by a subcutaneous implant of 5 mg. of the powdered

propionate and examined three weeks later along with the first control bird shown in the table. The remaining treated birds were injected daily for six weeks (Sundays excepted) with 2 mg. Testosterone propionate in oil of sesame, while the corresponding control birds received injections of oil of sesame only. The five injected birds and the corresponding five controls were birds bred in captivity in the Calgary Zoo where the injections were carried out.

Unilateral adrenalectomy was also carried out on five adult males which were examined four weeks later. Although only one of these birds showed definite signs of adrenal regeneration as shown by gland weight, the operation had no effect on testicular or penile weight. Quantitative details of this experiment are therefore not reported below.

TABLE 1

Seasonal changes in weight of testes and penis of adult male mallards.

Date	Body Weight Kgs.	Testes Weight		Penis Weight		
		g.	as % of body wt.	g.	as % of body wt.	
Feb. 10/55	1·080	0·100	·01	0·23	·02	Z
Feb. 10/55	1·108	0·16	·01	0·53	·05	Z
Feb. 17/49	1·130	0·27	·02	0·38	·03	Z
Feb. 23/54	1·085	0·16	·02	0·62	·06	Z
Mar. 9/50	1·250	0·60	·05	1·52	·12	Z
Mar. 17/49	0·954	0·56	·06	1·52	·16	Z
Apr. 1/54	1·156	1·53	·13	0·83	·07	Z
Apr. 7/54	1·115	0·32	·03	0·02	·001	
Apr. 15/49	1·245	3·49	·28	1·79	·14	
Apr. 25/49	1·220	9·74	·80	1·78	·15	
Apr. 30/49	1·000	21·00	2·10	1·70	·17	
May 1/49	1·166	23·90	2·05	2·50	·21	
May 1/54	0·945	3·82	·40	1·38	·15	
May 2/49	1·265	20·35	1·61	2·75	·22	
May 15/49	1·090	18·40	1·70	2·97	·27	
May 16/54	1·020	1·43	·14	0·83	·08	
May 16/54	0·900	0·42	·05	0·93	·10	
June 13/50	1·000	15·74	1·57	1·87	·19	
June 18/48	1·285	18·60	1·46	2·40	·19	Z
June 18/48	1·235	3·40	·28	1·25	·10	Z
June 18/48	1·100	8·0	·73	2·25	·21	Z
Aug. 14/54	1·300	0·20	·02	0·95	·07	
Aug. 17/54	1·190	0·344	·03	0·64	·05	
Aug. 23/48	1·030	0·19	·02	0·62	·06	Z
Sept. 25/54	1·325	0·22	·02	0·87	·07	
Sept. 26/53	1·01	0·14	·01	0·60	·06	
Nov. 5/53	1·02	0·16	·02	1·01	·09	
Dec. 20/51	1·168	0·43	·04	0·73	·06	Z

Birds marked " Z " had been kept up to several weeks in the Edmonton Zoo between capture and examination.

RESULTS AND DISCUSSION

1. *Seasonal changes in weight of testes and penis of adult mallards*

Table 1 and Fig. 1 show the body weights and the weights of the testes and penis of birds killed at various times of the year. The period during which microscopic examinations of the testes revealed complete spermatogenesis is also indicated in Fig. 1. As can be seen from Fig. 1, penis weights increase from a " resting weight " of about 0·6 gms. or about 0·05 per cent of body weight to a maximum of almost 3 gms. or about 0·3 per cent body weight at the height of the breeding season in late May. The peak of penile weight

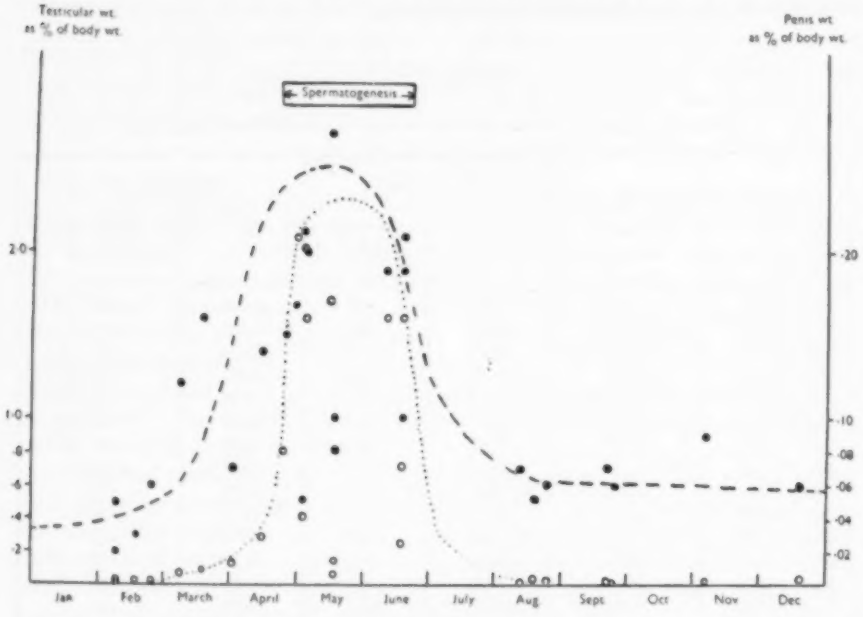


Fig. 1.—Seasonal changes in testicular weight and weight of the penis (expressed as per cent of body weight) in adult mallards. Open circles and dotted line testicular weights. Black circles and interrupted line weight of penis.

coincides with the peak of the testicular weight. Throughout a parallelism between testicular and penis weight is evident from the figures in Table 1, for example three males killed on May 1st, 1954 and May 16th, 1954 with rather small testicular weights for this season also had much lower penis weights than other birds with much larger testes killed in the same month. It may be noted that Champy *et al.* (1932, footnote, page 377) also suspected an annual penile recrudescence in wild ducks (presumably of this species) killed by hunters. The penis of immature males killed between late July and early November, Table 1a, which had all reached adult body size showed an average weight of only 0·03 gms. or 0·0026 per cent of body weight. Therefore, the penis of adults outside the breeding season weighs about twenty times as much as the

penis of prepuberal birds and during the breeding season shows a further and roughly five-fold increase in weight.

The fact that the penis of adults is larger at all seasons than that of immature birds may be due to the fact that in adults some androgen production probably occurs at all times of the year except in July and August, the period following

TABLE 1a

Body weight, weight of testes and penis of a group of juvenile male mallards.

Date	Body Weight	Testes Weight		Penis Weight	
		g.	as % of body wt.	g.	as % of body wt.
July 25/50	0·970	·06	·006	·05	·006
Oct. 10/53	1·100	·09	·008	·02	·002
Oct. 11/54	1·230	·08	·006	·03	·002
Oct. 11/54	1·355	·08	·006	·03	·002
Oct. 11/54	1·270	·07	·006	·03	·002
Oct. 11/54	1·125	·09	·008	·05	·005
Oct. 31/53	1·205	·09	·007	·01	·001
Nov. 5/53	1·160	·07	·006	·03	·003
Nov. 5/53	1·360	·08	·006	·02	·001
				mean ·032	·0026

the breeding season, for it was only at this period that Höhn (1947) found a minimal development of testicular interstitial cells.

2. *The effect of complete and partial castration on penis weight in adult mallards*

In Table 2 the body weights, testicular weights of controls and penis weights of ten complete castrates, eight incomplete castrates and six sham operated controls are reported. Complete castration resulted in an average penis weight approximately half of that found in the controls. The difference in the two mean values shown, 0·056 per cent of body weight in the complete castrates and 0·103 per cent of body weight in the controls is statistically significant; application of the t test gives a probability value of approximately 0·03.

The smaller difference in mean penis weights between the incomplete castrates and the controls is not statistically significant (probability value 0·2–0·3).

It should also be noted that the conditions of captivity appear to have inhibited testicular development in the controls since the maximal testicular weight was only a little over 2 gms. whereas wild birds in late April and May, Table 1, showed testes weighing over 20 gms. and penile weights close to 2 gms. Comparison of the castrates with controls showing full testicular development could therefore be expected to show a greater effect of castration on penile weight than was actually observed. However, the conclusion that complete castration early in the spring prevents the breeding season enlargement of the penis is warranted by the above results. A single bird castrated in November did not have a smaller penis than a control bird compared with

it four weeks later. The observation that early spring castration of adult wild mallards can prevent the breeding season enlargement of the penis, differs from the negative effect of this operation in adult domestic ducks reported by Champy *et al.* (1932) but it must be pointed out that these observers assessed penis size only by cloacal palpation.

3. *The effect of Testosterone administration on penis weight in adult mallards*

The effects of Testosterone administration on testicular and penis weight are shown in Table 3. The first two treated birds marked with an asterisk in Table 3 were given a subcutaneous implant of 5 mg. of Testosterone and were examined three weeks later. They should be compared with the first control bird, which was kept with them. The remaining five treated birds were injected with 2 mg. of Testosterone daily for six weeks and should be compared with the remaining controls which were injected with the solvent only (oil of sesame) which was used for the Testosterone injections.

From the results obtained earlier, Table 1, it was anticipated that by the end of February no appreciable testicular enlargement would be found in the controls. However, as is evident from Table 3, three of the control birds had testes weighing more than one gram, one bird having in fact a testicular weight as high as is normally found at the height of the breeding season, with spermatozoa evident in microscopic sections of the testes. As noted in the section Materials and Methods, these birds had been bred in captivity and this or the fact that some heat was provided in their living quarters may account for the unusually early testicular development found in some of the birds. The difference in mean penis weights of the treated and control groups 2·6 gms. 0·0250 per cent of body weight and 1·5 gms. and 0·169 per cent of body weight is not statistically significant, the probability value is approximately 0·25.

Nevertheless, some effect of the testosterone treatment on penis weight seems evident when the two implanted birds are compared with their control and in the fact that whereas penis weight in all injected birds was at least 0·2 per cent of body weight whereas it was below this value in four out of the six controls.

It is clearly difficult to demonstrate the effect of testosterone administration on penis weight when treated birds are compared with a control group which includes birds with enlarged testes which were presumably producing androgen. Therefore, the treated birds are also compared with only those of the controls from Table 3 which had a testicular weight less than one gram, plus the first four birds killed in February taken from Table 1 which had also been kept in captivity before examination. Such a comparison of the seven Testosterone treated birds with seven controls gives the following results :

	Mean Penis Weight	
	g	Percentage of body wt.
Treated birds :	2·6	0·25
Controls :	0·7	0·06

TABLE 2

The effect of castration on penis weight in adult mallards. The months indicate the period when the birds were examined, operations were performed 4–6 weeks earlier.

Month	Complete castrations			Incomplete castrations			Controls (sham operated)			
	body wt. Kg.	penis wt. g.	penis wt. as % of body wt.	body wt. Kg.	penis wt. g.	penis wt. as % of body wt.	body wt. Kg.	testes wt. g.	penis wt. g.	penis wt. as % of body wt.
March	1·07	0·7	0·065	0·9	0·4	0·044	1·25	0·6	1·5	0·12
	0·97	0·2	0·022	0·96	0·6	0·067	0·95	0·6	1·5	0·16
	1·2	0·3	0·025	1·14	0·6	0·053				
	1·03	0·8	0·078	1·18	0·9	0·076				
				0·84	0·9	0·119				
April	0·8	0·9	0·112				1·13	2·01	1·195	0·11
	1·0	0·19	0·019				0·92	0·99	0·296	0·03
	1·05	0·66	0·063				1·15	2·29	1·273	0·11
May	0·89	0·4	0·045	0·95	1·2	0·126	1·2	1·4	0·9	0·09
	0·96	0·6	0·063	0·95	0·7	0·074				
	0·86	0·9	0·105	1·02	0·5	0·049				
	mean penis wt.	0·565	0·056	mean penis wt.	0·722	0·075	mean penis wt.		1·11	0·103

TABLE 3

The effect of Testosterone administration on penis weight in mature mallards.

Treated					Controls				
Body wt. Kg.	Testes wt. g.	Testes wt. % of body wt.	Penis wt. g.	Penis wt. % of body wt.	Body wt. Kg.	Testes wt. g.	Testes wt. % of body wt.	Penis wt. g.	Penis wt. % of body wt.
*1·13	0·4	0·035	1·1	0·097	1·13	0·3	0·03	0·4	0·035
*1·13	0·6	0·053	1·1	0·097	1·18	2·6	0·22	2·2	0·190
1·3	0·5	0·038	3·1	0·240	0·9	0·2	0·02	1·2	0·120
1·07	0·4	0·036	2·2	0·210	1·2	20·0	1·67	3·4	0·28
1·22	0·4	0·033	3·1	0·260	1·04	7·8	0·78	2·8	0·27
1·08	0·7	0·063	5·5	0·510	0·83	0·4	0·04	1·0	0·120
1·25	0·6	0·05	3·0	0·240					
Mean penis wt.			2·6	0·250	Mean penis wt.			1·5	0·169

The two birds marked with an asterisk were given a subcutaneous implant of 5 mg. Testosterone propionate and examined three weeks later. The remaining treated birds were injected daily for six weeks with 2 mg. of Testosterone propionate. All birds were examined in February.

These results indicate a significant effect of Testosterone injections on penis weight. Another conclusion which follows from the results obtained with Testosterone administration is that at the height of the breeding season male mallards produce androgens equivalent to more than 2 mg. of Testosterone per day, since none of the injected birds showed the enlargement and coiling of the vas deferens which is found in normal birds at the height of the breeding season.

ACKNOWLEDGMENTS

This work was supported by a grant from the Medical Research Fund of the University of Alberta. The help of various individuals in Calgary and Edmonton, particularly of Mr T. Baines, Curator of the Calgary Zoological Gardens, in the procurement of live mallards and their maintenance is gratefully acknowledged.

REFERENCES

Benoit, J. (1950). In Grassé, P. *Traité de Zoologie*. **15** Oiseaux : 463. Paris : Masson et Cie.

Champy, C., Buliard, H., Kritch, N. & Demany, M. L. (1932). Étude du mécanisme de developpement de quelques caractères sexuels des oiseaux. *Arch. Anat. micr.* **27** : 301.

Höhn, E. O. (1947). Sexual behaviour and seasonal changes in the gonads and adrenals of the mallard. *Proc. zool. Soc. Lond.* **117** : 281.

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1943). *The handbook of British birds*. **4**. London.

Wolff Et. & Wolff Em. (1948). Sur le determinisme de la differenciation du penis chez le Canard. *Arch. Anat. micr.* **37** : 155.

COLLEMBOLA SYMPHYPLEONA FROM THE GAMBIA, WITH A NOTE ON THE BIOGEOGRAPHY OF SOME CHARACTERISTIC SAVANNA FORMS

BY

D. H. MURPHY*

Department of Zoology, Durham Colleges in the University of Durham

[Communicated by Miss Theresa Clay—Accepted 10th November 1959]

(With 132 figures in the text)

Twenty species of Symphypleona are recorded from the Gambia of which twelve are new to science and are described. A brief survey is given of the chief vegetation and soil types to assist in classifying the habitat references in the text. *Sminthurinus stenognathus* Börner and *Bourletiella spathacea* Börner are noted as probably extending throughout the northern savanna belt of the Ethiopean region, having been recorded from both ends of this vegetation zone. *Sminthurides cf. ramosus* and *Sminthurus macroceros* Denis are recorded as occurring on both sides of the Atlantic and it is suggested that resistant stages which allow them to live under savanna conditions also fit them for long distance wind dispersal. In an appendix (*vide infra*) some information is given on some species of *Sminthurides* for comparison with species newly described here, and lectotypes are established for *S. melanotus* and *S. spegazzinii* from material in the British Museum collection.

CONTENTS

	Page
Introduction	557
The systematic description of the Symphypleona collected	558
Comments on the distribution of some forms	589
Acknowledgments	591
Appendix	591
References	594

INTRODUCTION

While working on Culicidae at the Medical Research Council Laboratories in the Gambia, the opportunity was taken to do a certain amount of general collecting of entomological material, paying especial attention to the soil fauna. Apart from insects of direct medical or economic importance, very little is known about the insect fauna of this region, which is emphasized by the fact that of the twenty species of Symphypleona mentioned here, twelve are new to Science.

This paper is the first of a series on the Collembola of the territory and the present collection appears to be the first of any size so far made in the north savanna belt of the African continent. Material from other groups has been passed on to appropriate specialists. The whole of the material described here was collected between May 1956 and March 1958.

The Gambia consists of a narrow strip of country bordering the large Gambia river from its mouth for a distance (by river) of about 600 Km. It lies 13·5° north of the Equator and has a tropical climate with one well defined

* Present address c/o Dept. of Zoology, University of Malaya in Singapore, Bukit Timah Rd., Singapore 10, Malaya.

rainy season extending from June to October, during which approximately 1000 mm. of rainfall occur. The area from which the greater part of the collection was made, was the vicinity of the village of Keneba in the West Kiang district of the Gambia Protectorate (Senegal Grid 45/984 364) where the Medical Research Council has a permanent field station. Some geographical information is available in Gamble (1949), McGregor & Smith (1952) and Bertram *et al.* (1958) but for general ecological purposes this needs amplification. The village lies 80 Km. directly inland from the coast, about 10 Km. from the river and at about 25 m. above sea level. The bulk of the terrain is covered by wooded, tall-grass savanna together with the various stages of cultivation and bush fallow involved in the shifting agriculture practised locally, or by the extensive mangrove swamp and sand-flat complex associated with the subsidiary tidal creeks of the river. Marginal to the latter are freshwater swamps (usually only with water for part of the year) which are often cultivated for rice, together with small areas of fringing high forest where the water table remains close to the surface even during the dry season. These appear to be developed mainly on gleyed alluvial soils and the upper horizons may be rich and highly organic. In the savanna are typical pisolithic tropical red-earths, evidently of very long standing and frequently including great accumulations of the ironstone concretions which characterize such soils, (locally and incorrectly termed " laterite ").

The use made of the collection is at present mainly taxonomic, and the above notes are intended to help in classifying the habitat references in the text of this and subsequent communications.

In the descriptive section which follows, certain abbreviations standard in collembolan taxonomic literature are employed. Thus PAO is short for Post Antennal Organ, S.O. Ant. III for the sense organ of Antenna III and EA for empodial appendage. The usual procedure of indicating relative dimensions by arbitrary and not always interchangeable units is not followed. Instead, the size of a particular individual is quoted at the beginning (with an indication of maximum size if this differs) and all subsequent measurements in microns are understood to refer to this specimen.

Since in the preparation of description and illustration it is my practice to dissect the material and since in my opinion, it is preferable to use an intact specimen as holotype, it has not always been practicable to use as holotype the specimen from which the bulk of the figures were prepared. In such instances the dissected specimens have been subsequently mounted in Salmon's P.V.A. media and included among the paratype material deposited in the British Museum.

SYSTEMATIC DESCRIPTIONS OF THE SYMPHYPLEONA COLLECTED

Fam. Neelidae

MEGALOTHORAX MINIMUS Willem

All material of the genus encountered has been referred to this species. Judging by the localities from which it has been recorded, it is confined to soils which remain moist throughout the year

E.g. Surface litter of gleyed soils under fringing forest, rice fields 3 Km. west of Keneba. 31. vii. 57.

Dark organic soil under banana trees. Manduar village (West Kiang). 21. viii. 57.

Sandy alluvium near Kotu Stream. Fajara (Kombo) 20. iii. 58.

Fam. Sminthuridae

Sminthurides

Three of the four known subgenera are represented, *Sminthurides* by four species, *Sphaeridia* by two and *Denisiella* by one.

SMINTHURIDES s.str.

It has been found expedient in the following descriptions to employ characters not always available in the literature dealing with previously described forms. In cases where these are applied as a distinction from species not occurring in the Gambia it has been found necessary to supplement descriptions of the gambian material with certain details of such other relevant species as have been available to me. An important characteristic appears to be the number and shape of the pregenital setae of the female, i.e. the setae on the anterior (ventral) valve of the genital pore. In the appendix (*vide infra*) all the species that I have so far been able to examine, are classified according to this feature. No simple way exists of describing in print, details of the chaetotaxy of the dens or tibiotarsus. In most instances therefore, an illustration has been given, but attention is drawn to the number of setae in the inner lateral row of the dens which is readily identifiable and to the presence of many or few in the outer lateral row, a feature likely to be of importance in the quinquearticulate species. Murphy (*in litt.*) has attempted a classification of the processes of the male antennal clasping organ and the same nomenclature is employed in the present paper. In *Sminthurides* s.str. the basic plan appears to be as follows. On Antenna II one proximal sensilla p^1, three median (m^1 to m^3) and one distal (d^1). On Ant. III there is one proximal (p^1) a median complex consisting of a depression containing several sensillae and two distal processes, a large spine (d^1) and a sensilla posterior to this (d^2) very variable in shape and of great taxonomic value. The S.O. Ant. III is on the anterior face of this segment. In various species, supplementary sensillae may be added to this basic plan in most of the positions indicated. Other subgenera differ markedly in the organisation of the clasping organ and it is likely that this will ultimately prove the basis of subgeneric classification. It may be noted at this point that S. *sphaeridioides* (*vide* page 566) may then have to be separated subgenerically.

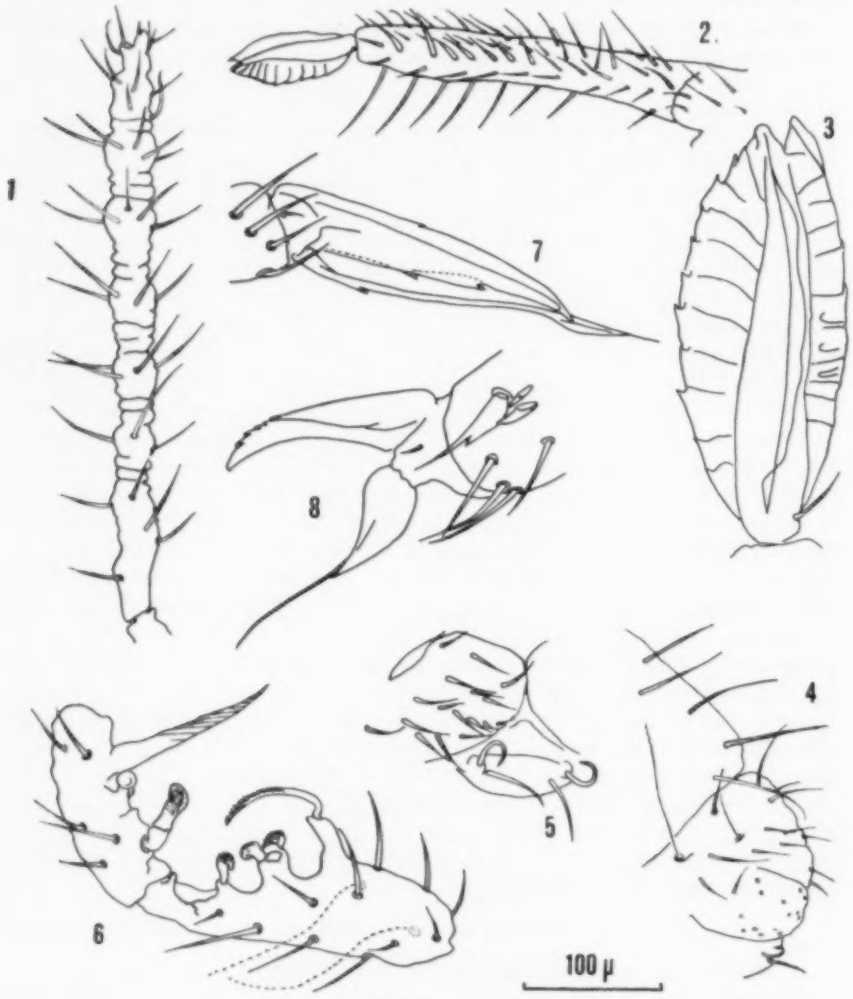
SMINTHURIDES GAMBIAE sp.n.

(Figs. 1 to 8, 18 and 117.)

Female : Size 0·75 mm. Colour yellowish green, suffused laterally with bluish pigment. Legs pale with violet tips, antennae with segs. III and IV violet pigmented.

Body with rather distinct segmentation of the thoracic region. Longest posterodorsal setae of great abdomen 95 μ, approximately equal to mucro (Fig. 9.) Anterodorsal (i.e. near midline on the metanotal fold) 57 μ. Longest

(anteromedial) setae of anogenital segment 53 μ. Genital setae (Fig. 5) 2 +2 the outer pair strongly hooked, the inner thickened and slightly curved. Antennae 1·7 head diagonal, with segments in the ratio 45 : 60 : 140 : 275 μ. Ant. IV (Fig. 1) with 7 subsegments of which the intermediate ones each have basal and apical subsegments as described by Stach (1957) for *S. penicillifer*.



Figs. 1 to 8—*S. gambiae*

Fig. 1.—Antenna IV of female, × 1·7 ; 2, Dens, dorsal view, × 1·7; 3, Mucro ventral view, × 3·0 ; 4, Anogenital segment, lat. view, × 1·0 ; 5, Lower anal valve and pregenital setae, × 1·7 ; 6, Male antennal clasping organ, × 2·4 ; 7, Claw I of female, × 3·0 ; 8, Claw III of female × 3·0 .

(All magnifications quoted are relative to the scale included in the illustration.)

Ant. III with sense organ of two minute sensillae in separate but closely adjacent pits. Ant. I with anterior cleft of which the upper margin is not emarginate. Ocelli 8+8 of which two are reduced. Leg I with tibiotarsus, outer edge of claw and empodial appendage 156, 76 and 84 μ resp. Claw I (Fig. 7) long and narrow with two inner teeth each on a separate shallow lamella which join just distally to the distal tooth. Two small outer teeth but no teeth on the lateral lamellae. Empodial appendage with strongly reduced lamella (19 μ) and with very elongate filament closely appressed to the claw which it overhangs, and unilaterally expanded into a lanceolate lamella at the tip. Leg II with tibia, outer edge of claw and EA as 163, 84 and 91 μ resp., with foot similar in structure to leg. I. Leg III with tibia, claw and EA as 198, 57 and 60 μ. Claw III (Fig. 8) without inner or outer teeth but with a pair of basal laterals and at the apex with a series of strong lateral denticulations. EA with large basal lamina and with long acuminate filament reaching well beyond the claw. Tibiotarsal organ with wide lamella on the guarding seta and with the proximal sac much the smaller of the two. Dens with dorsal chaetotaxy as in Fig. 2. There are 7 to 8 inner lateral setae on the dens of which the most distal is 65μ, or well over half the length of the mucro. Dens 266 μ or 2·7 length of mucro. Mucro (Fig. 3) 95 μ long and 46μ wide, with broad lamellae. Shaft terminating in a blunt free tooth. Inner lamella with 9 to 10 teeth, reaching apex : outer smooth throughout most of its length, but terminating in a membranous tooth without reaching apex. Ventral lamella smooth and reaching apex without a tooth. Mucronal seta present 17 μ, about 0·2 length of mucro. Tenaculum with one apical and two anterior setae on the corpus, with 3+3 teeth on rami and with basal appendages.

Male : 0·5 mm. Claw III narrower than in female and without the apical lateral denticles. Mucro shorter and rounder but outer lamella normal, ending just short of apex. (*cf. avicenniae*) EA I and II have the lanceolate tip less pronounced than in female. Antennal clasping organ as in Fig. 6. There are no supernumary sensillae in any position. On seg. II, p^1 is ciliated dorsally as are the three sensillae of the median group and the single distal d^1. On the anterior face, the two bothriotrichia are both long, slender and smooth. Ant. III with p^1 spoonlike and ridged, d^1 spirally striated in the distal half and d^2 in the form of a spherical, thin-walled sensillum on a papilla. Proximal to the bases of the distal processes are the usual three, simple sense hairs. Metanotal vesicles are present.

Affinities : *S. gambiae* is evidently very closely related to *S. melanotus* Börner 1907 from Argentina. Fortunately a specimen exists in the collection of the British Museum and examination shows that the two species are quite distinct. In the appendix a brief supplementary description of this specimen of *melanotus* (here established as lectotype) is given and *S. gambiae* can be distinguished by having two inner teeth on Claw I and by the much longer posterodorsal chaetotaxy.

Types : Holotype female and cotype male in alcohol, together with paratypes both in alcohol and mounted on slides, have been deposited in the British Museum (Nat. Hist.).

Type Locality : Basse (Upper River Division), Gambia, 19. x. 57. Surface of fresh-water pool near Mansajang. Also recorded from Keneba, Gambia 28. ix. 57 in fringing *Eleocharis* swamp and from Jali, Gambia 18. viii. 57 surface of pools in gallery high forest (2 Km. north of Jali).

SMINTHURIDES AVICENNIAE sp.n.

(Figs. 9 to 17 and 118.)

Female : Size 0·60 mm. (max. 0·7). Colour yellowish green with a strong and highly characteristic pattern of blue-black pigment and in extreme cases can become almost completely black (Fig. 118). Body with rather distinct segmentation of the thoracic region. Longest posterodorsal setae not thickened, 38 to 40 μ, less than half length of mucro (Fig. 10). Anterodorsal 27 μ, and longest (medial setae) of anogenital segment 38 μ. Pregenital setae (Fig. 17) 2+2 with inner much the stronger and the outer strongly curved but not hooked as in *gambiae*. Antennae 1·6 head diagonal with segments in the ratio of 42 : 50 : 133 : 209 μ. Ant. IV divided into 7 subsegments (Fig. 11) with intermediate annulations as in *gambiae*. Ant. I with anterior cleft not having the upper margin emarginate into a tooth. Ocelli 8+8 of which 2 are reduced. Leg I with tibiotarsus, outer edge of claw and EA 153, 70 and 38 μ resp. Claw I (Fig. 15) long and narrow, with faint trace of an inner tooth and with two small lateral teeth. EA slightly more than half length of inner edge of unguis, not differentiated into distinct lamina and filament. Leg II with tibia, claw and EA 133, 76 and 38 μ resp., claw morphologically as on leg I. Leg III with tibia, claw and EA, 160, 57 and 57 μ resp. Claw III (Fig. 14) without teeth of any kind, very slender. Empodium with large lamina and acuminate, filiform filament extending well beyond the claw. Tibiotarsal organ with two equal sacs and simple, non-lamellate guarding seta which extends beyond the end of the tibiotarsus. Furca with dorsal chaetotaxy as in Fig. 13 and ventrally as in Fig. 12, with 6 setae in the inner lateral row, the longest being 49 μ or slightly less than half length of mucro. Dens 285 μ or 2·7 length of mucro. Mucro (Fig. 18) relatively large and broad (106 by 57 μ) more than half as wide as long, with inner lamella having 8 to 10 teeth. Outer lamella wide, sinuate, untoothed and ending before the end of the shaft, but not expanded laterally with a tooth. Ventral lamella, wide and sinuate, smooth and reaching end of shaft. Mucronal seta present, 19 μ. Tenaculum as in *gambiae*. Ventral tube with 1+1 setae on valves.

Male : 0·45 mm. Mucro differs from that of the female in having the outer lamella ending only 3/4 along the shaft as described for *S. penicillifer*. Antennal clasping organ (Fig. 16) very similar to that of *S. gambiae*, without sensillae additional to the basic plan for *Sminthurides* s.str. Bothriotrichia both long, slender and smooth. It differs in having d^1 on Ant. III distinctly striated to the base and the spherical sensilla of d^2 relatively smaller. Metanotal vesicles present.

Affinities : The nearest forms to this appear to be *S. gambiae* and *S. melanotus* from which the structure of the claws, simple guarding seta of the tibiotarsal organ, short posterodorsal setae, unhooked genital setae and many other features mentioned in the above description make it easily distinguishable.

Types : Holotype female and allotype male in alcohol, together with paratypes both in alcohol and mounted on slides, have been deposited in the British Museum (Nat. Hist.).

Type Locality : Keneba, Gambia, 5. ii. 57. Surface of water and of *Avicennia* pneumatophores. Mangrove swamps 2·5 Km. west of Keneba.

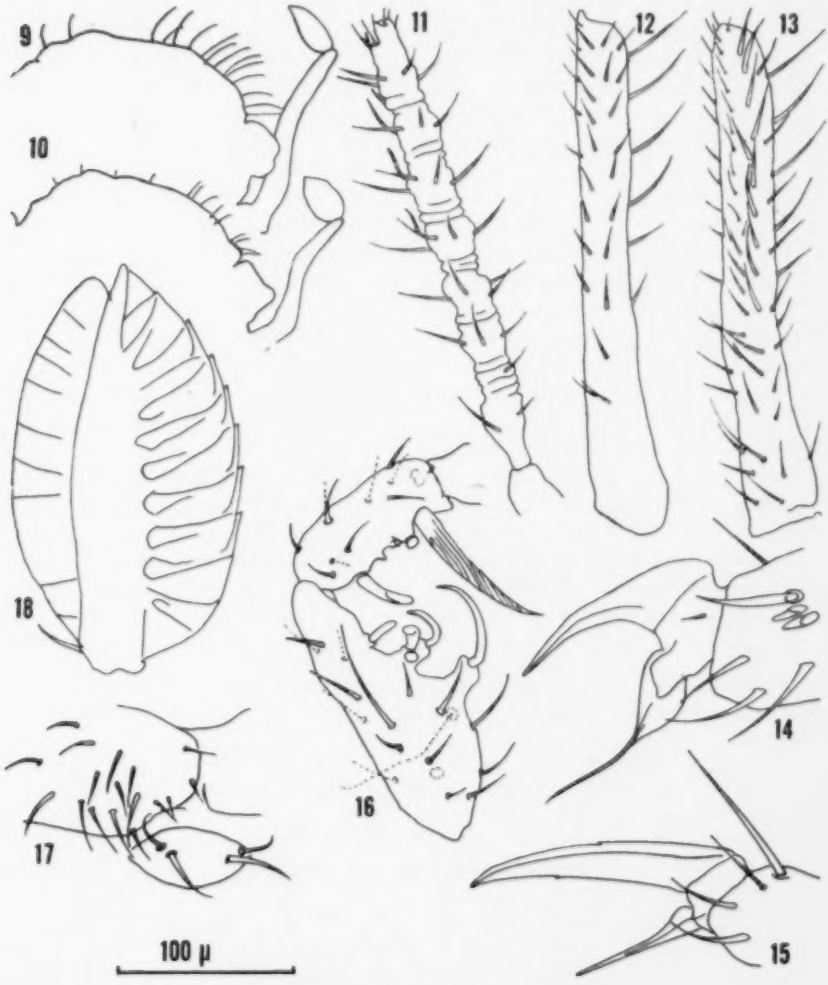


Fig. 9.—*S. gambiae* profile. Figs. 10 to 18.—*S. avicenniae.*

Fig. 10.—Profile ; 11, Ant. IV of female, × 1·3 ; 12, Dens, ventral view, × 1·0 ; 13, Dens, dorsal view, × 1·0 ; 14, Claw III, × 2·4 ; 15, Claw I, × 2·4 ; 16, Antennal clasping organ of male, × 1·9 ; 17, Lower anal valve and pregenital setae, × 1·3 ; 18, Mucro, × 2·4. (All magnifications quoted are relative to the scale included in the illustration.)

SMINTHURIDES MACGREGORI sp.n.

(Figs. 19 to 27.)

Female : 0·45 mm. Coloration yellow buff, with blue pigmentation laterally, including the leg-bases and with a mid-dorsal spot or stripe (Fig. 27). Specimens from temporary swamp in Savanna 10: viii. 57 and are more strongly pigmented. Body globular with indistinct indications of segmentation. Longest posterodorsal setae 34 μ just over half length of mucro, anterodorsal 15 μ, longest hairs of the anogenital segment equal to or slightly longer than the posterodorsal setae of the great abdomen. Anogenital setae (Fig. 26) 2+2, simple and tapering. Antennae 1·2 head diagonal, with segments 23, 34, 71 and 129 μ resp. Ant. IV divided into 5 simple subsegments which are 42, 19, 19, 15 and 34 μ resp. the basal therefore being considerably less than twice the apical. Ocelli 8+8 of which two are reduced. Leg I with tibia, outer edge of claw and EA, 95, 40 and 39 μ resp. Claw I (Fig. 24) narrow with one inner tooth but no outer or lateral teeth. Unguiculus with narrow lamina and long, acuminate filament exceeding the claw. Leg II with tibia, claw and EA as 90, 38 and 38 μ resp., the claw similar to the front pair. Leg III with tibia, claw and EA as 99, 30 and 30 μ resp., the claw (Fig. 25) with inner but no lateral teeth and EA with a large lamina and simple, acuminate filament exceeding the claw. Tibiotarsal organ with slightly unequal sacs and with lamellate guarding seta. Furca with chaetotaxy as in Figs. 19 and 20, having 3 setae in the inner lateral row and many (about 9) in the outer lateral row. Dens 141 μ, and the longest seta of the inner row is 30 μ, thus being less than half length of mucro. Mucro (Fig. 22) 65 μ long with moderately broad lamellae, the inner having 10 to 11 teeth. Outer lamella smooth and terminating without reaching the apical tooth of the shaft, though not expended or toothed at this point. Ventral lamella smooth and extending to the apex of the shaft. Mucronal seta present, 15 μ. Tenaculum with one apical and two anterior setae on the corpus, 3+3 teeth on the rami and with basal appendages.

Male: Unknown. Since three separate populations have been examined, from different dates and all involving a fair number of specimens, the possibility exists that this species may be parthenogenetic.

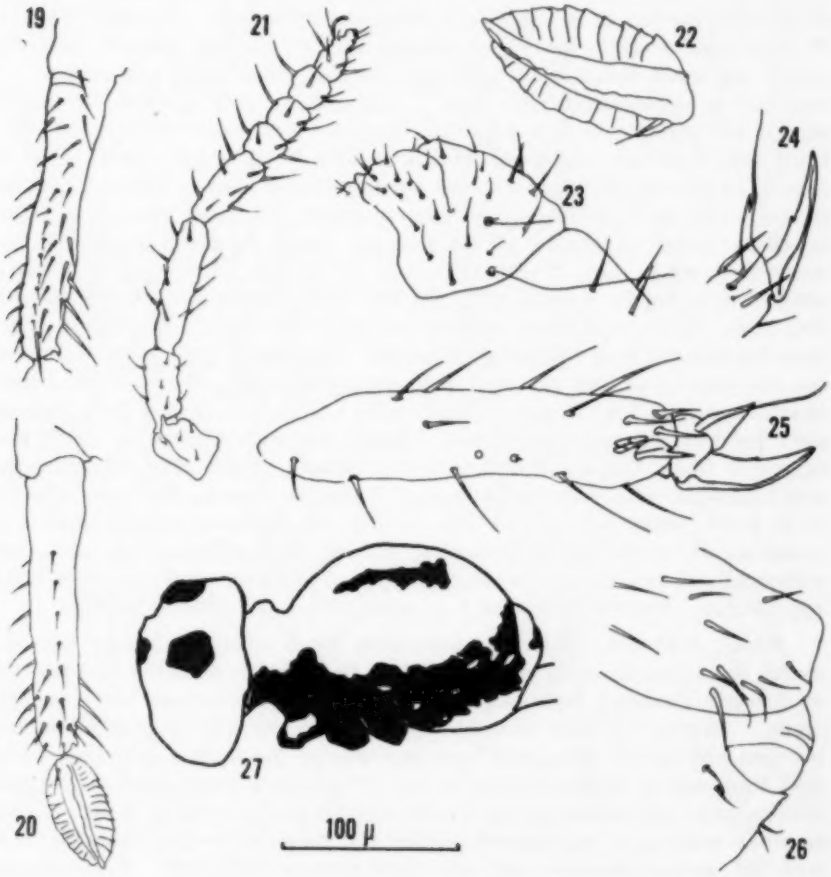
Affinities : Among the "quinquearticulate" group are a number of inadequately known species and a revision is urgently required. Certain of the characters are difficult to use and one important feature, the relative size of the antennal subsegments appears to be subject to allometric growth, although among fully adult animals it appears to be valid. *S. macgregori* differs from *S. inequalis* Börner by the lamellate guarding seta and from *S. terrestris* Maynard by the absence of well-marked lateral teeth. From *parvulus* (Krausbauer) the shape of the mucro is quite distinctive but attention may be drawn to the main distinguishing features of value in the group. Thus *S. parvulus* has only 1+1 genital setae in the female, the tibiotarsal guarding seta has the lamella terminating in several fringes, the longest posterodorsal setae are almost equal to the mucro in length and the tenaculum has only 2 anterior setae on the corpus. The chaetotaxy of the dens is also highly distinctive and

details of this will be available in a forthcoming publication (Murphy *in litt.*).

I am pleased to be able to dedicate this species to Dr I. A. McGregor under whose direction my work in the Gambia was carried out.

Type locality : Eleocharis swamp developed on sandflats which during the rainy season become inundated by fresh water, 2 Km. south of Keneba (West Kiang district of Gambia Protectorate). 28. ix. 57.

Temporary pools in road near Jali (W. Kiang) 18. viii. 57.



Figs. 19 to 27.—*S. macgregori.*

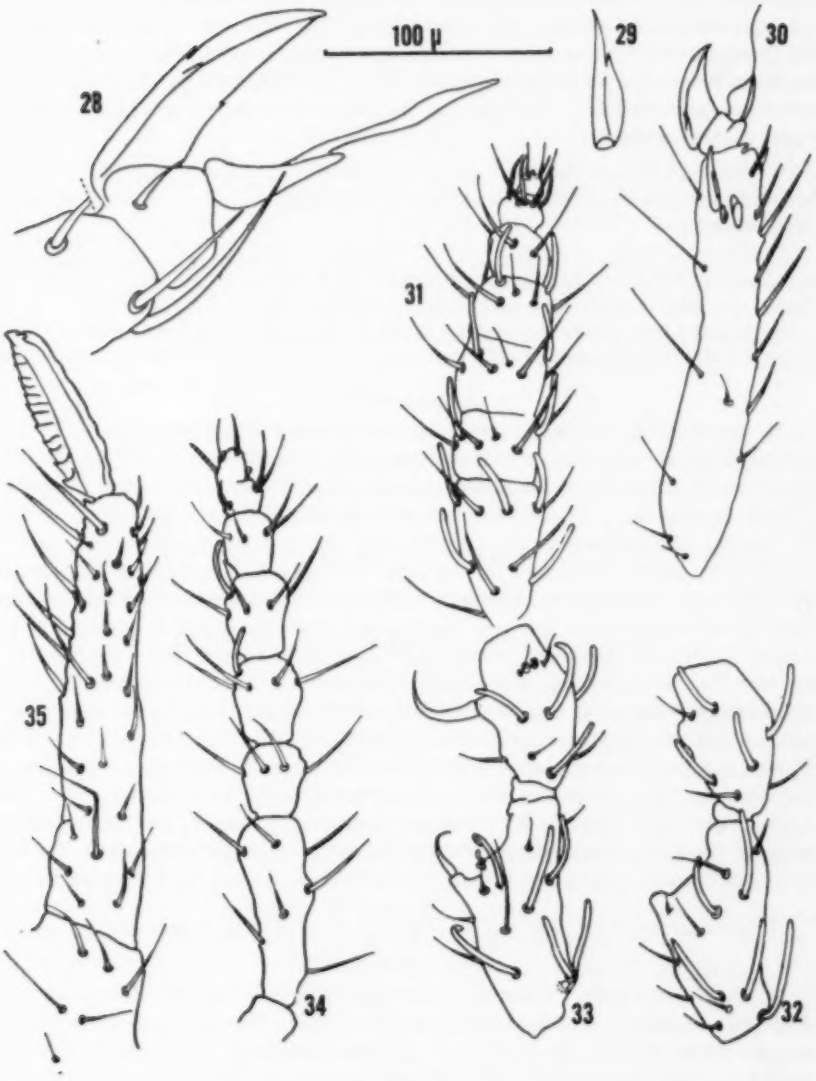
Fig. 19.—Dens, dorsal view, × 1 ; 20, Dens, ventral view, × 1 ; 21, Antenna, × 1 ; 22, Mucro, × 2·2 ; 23, Anogenital segment, lateral view, × 1 ; 24, Claw I, × 2·2 ; 25, Tibiotarsus and claw III, × 2·2 ; 26, Lower anal valve and pregenital setae, × 2·2 ; 27, Distribution of dark pigment on the body (specimen from temporary swamp in savanna—10. viii. 58). (All magnifications quoted are relative to the scale included in the illustration.)

SMINTHURIDES SPHAERIDIOIDES sp. n.
(Figs. 28 to 35)

Female : 0·4 mm. Coloration pink with lateral blue pigmentation which is continuous round the hind part of the body. Eye spots large. Longest posterodorsal setae not thickened, up to 38 μ which is 0·8 length of mucro. Longest setae of anogenital segment the same. Pregenital setae 2 +2, simple and acuminate, the inner rather longer than the outer. Antennae 1·1 to 1·2 head diagonal with segments in the ratio 23 : 38 : 61 : 133 μ. Antenna IV (Fig. 34) divided into six simple subsegments of which the basal is about three times the length of the very small apical subsement. Subsegs. III and IV each bear a single thinwalled sensilla and VI bears a strongly capitate pin in the outer notch. Ant. III with normal sense organ and having no tendency to subsegmentation. Ant. I with anterior cleft of which the upper edge is not emarginate into a tooth. Ocelli 8 +8 of which two are reduced. Leg I with tibiotarsus, outer edge of claw and EA 80, 25 and 27 μ resp. Claw I (Fig. 28) with a single inner tooth and a pair of lateral teeth. EA with lamella of about 12 μ and a stout clavate filament which overhangs the claw (*cf.* the lamellate apical expansion of the filament found in *gambiae*, *penicillifer*, *spegazzinii*, etc.). Leg II with tibia claw and EA as 76, 25 and 30 μ resp., the foot as on leg I. Leg III (Fig. 30) with tibia, claw and EA as 95, 23 and 25 μ resp. Claw with basal lateral but no inner teeth. Empodium with large lamina and long acuminate filament. Tibiotarsal organ with proximal sac the smaller of the two and with lamellate spine. Furca with dorsal chaetotaxy as in Fig. 35 and ventrally with 1, 1, 1, 1, 2, 3, 3, 1 from base to apex between the two lateral rows. Inner row with 5 setae of which the longest is 19 μ. Outer row of 6 to 7 short setae. Mucro (Fig. 35) 46 μ long and 11 μ wide, with mucronal seta 7 μ. Lamellae narrow, the inner with 10 to 11 teeth, outer and ventral both smooth but the outer lamella ends in a membranous tooth without reaching end of shaft. Tenaculum with one subapical and two anterior setae on corpus, 3 teeth on rami and with basal appendages. Ventral tube with 1 +1 setae (10 μ) and without papillae.

Male : 0·25 mm. Most characteristics agree with the female but the mucro is shorter, inner lamella with 7 to 9 teeth, claws narrower and EA not so strongly clavate. Metanotum with vesicles and antennae with clasping organ. This is of a most unusual type (Figs. 32 and 33). It is intermediate between the simple *Sphaeridia* type and that of the normal *Sminthurides* in that there are no bothriotrichia on Ant. II where furthermore the proximal process is a *Sphaeridia*-like spine, the median group consists of two simple sensillae without a well-defined papilla and there is no distal sensilla. On Ant. III, as in *Sphaeridia* only the distal spine is developed. Furthermore, antenna II bears ten long, thin-walled sensillae, Ant. III bears seven and Ant. IV (Fig. 31) shows distinct signs of subsegmentation with sensillae on most subsegments.

Affinities : There appear to be no close relatives to this species among those of which the male is known. Among species with simple subsegmentation of Ant. IV in the female no others are known to have six subsegments. On



Figs. 28 to 35.—*S. sphaeridioides.*

Fig. 28.—Claw I, × 2·7; 29, Guarding seta, × 2·7; 30, Tibiotarsus and claw III, × 1; 31, Male antenna IV, × 1; 32, Male antenna II & III, posterior, view, × 1; 33, Male antenna II & III, anterior, view, × 1; 34, Female, antenna IV, × 1; 35, Dens of female, dorsal view, × 1.

(All magnifications quoted are relative to the scale included in the illustration.)

geographical grounds it would be interesting to know more about *S. tropicus* Delamare 1952 of which the male is as yet unknown. Although distinct from *S. sphaeridioides* in having only 5 subsegments in Ant. IV, only 4–5 teeth on the inner lamella of the mucro and in partial subsegmentation of Ant. III, the form has some points of similarity, e.g., in shape of empodial appendage and may prove to be another species to possess the aberrant type of clasping organ in the male.

Types : Holotype female and allotype male in alcohol, together with a series of paratypes have been deposited in the collection of the British Museum (Nat. Hist.).

Type locality : Keneba, Gambia, 2. x. 57. Cultivated red earth soil from beneath dense herbaceous vegetation, fallow groundnut farm just outside the Medical Research Council field station. Six adult females, three adult males, several juveniles.

Also recorded from Gallery Forest 2 Km. north of Jali, West Kiang, in very organic, coprogenous soil in dried up stream bed, 17. vi. 57.

SPHAERIDIA

In the Gambia, material has been encountered which is referable to two completely distinct forms which can be easily separated between themselves. The relation which these bear to previously described species is however more difficult to express. Thus Polish material described by Stach under the name *S. pumilis* (Krausbauer) has only lightly serrate tibiotarsal setae, simple non-swollen outer distal seta on the dens and posterodorsal setae " as long as the mucro ". *S. serratus* (Folsom & Mills) has " a patch of long, heavy pointed bristles on the posterior dorsum, the longest more than half the length of the mucro ". Of the gambian forms, one species is tentatively referred to *S. serratus* Folsom in having, when fully adult (and only then) two heavy, closely appressed serrate setae on the inner side of the dens and in that it agrees with extensive British material referred to this form in the chaetotaxy of the dens. British and Gambian material of *Sphaeridia* both have the outer distal seta of the dens strongly swollen at the base and the appressed tibiotarsal spines with strong blunt serrations. In Gambian material, however, the posterodorsal setae of the furcal segment are consistently shorter than half length of mucro (for which reason they are given a varietal name here, var. *brevipila* nov.).

S (SPHAERIDIA) CF. SERRATUS (Folsom & Mills) var. BREVIPILA, nov.

(Figs. 36 and 42)

Female : 0·4 mm. Coloration uniform pinkish violet. Body globular with segmentation of thorax almost obliterated. Anterodorsal setae sparse, simple, 10 to 12 μ, long (Fig. 36). No pregenital setae. Antenna 1·2 head diagonal, with segments 18, 31, 28 and 85 μ resp. Antenna IV simple, not annulated. Antenna I with anterior cleft but not emarginate into a tooth. Ant. III with sense organ of two very small sensillae in separate but closely adjacent pits. Eyes 8+8 as in *pumilis* sensu Stach. Leg I with tibiotarsus, outer edge of claw and EA and on leg III 85, 18 and 8 μ resp. Claw I and II with distinct inner tooth, outer tooth and one pair of laterals and with narrowly lamellate empodial appendage of which the filament exceeds the inner edge

of the claw. Claw III with no inner tooth, but outer and lateral teeth present, and EA with broad lamellae and no filament. Tibiotarsus without tibiotarsal organ, chaetotaxy (in fully adult specimens only) as in *S. serratus*. (This is also true of all British material examined of this genus.) Dens (Fig. 42) with three inner, enlarged setae and with a swollen apical seta (s) on the outside (this is true also in the case of British material referred to *S. serratus* but is apparently not the case in the Polish *S. pumilis* examined by Stach 1956). The dens is 77 μ long and the longest inner seta is 13 μ, less than one third length of mucro. Mucro very narrow, 43 μ long with serrate inner lamella and smooth outer lamella. At about half-way this diverges sharply outwards from its former course, while a short separate lamella on the same course ends just proximal to this point in a sharp tooth. This feature is less distinct than in *S. proxima* (*cf.* Fig. 41) but the mucro of both species is essentially similar in structure. No mucronal seta. Tenaculum with three subapical setae on the corpus, 3 : 3 teeth on the rami and with basal appendages. Ventral tube with 1 : 1 setae on the valves, 10 μ.

Male : 0·25 mm. Metanotal vesicles absent. Antennal clasping organ (Fig. 41) with the spine of ant. III considerably larger and stronger than that of seg. II (note that in the figures, the specimens are so orientated as to show the full length of the *smaller* spine in each instance).

Type locality : Dark organic soil in banana grove, Manduar village (West Kiang district of Gambia protectorate). 21. viii. 58.

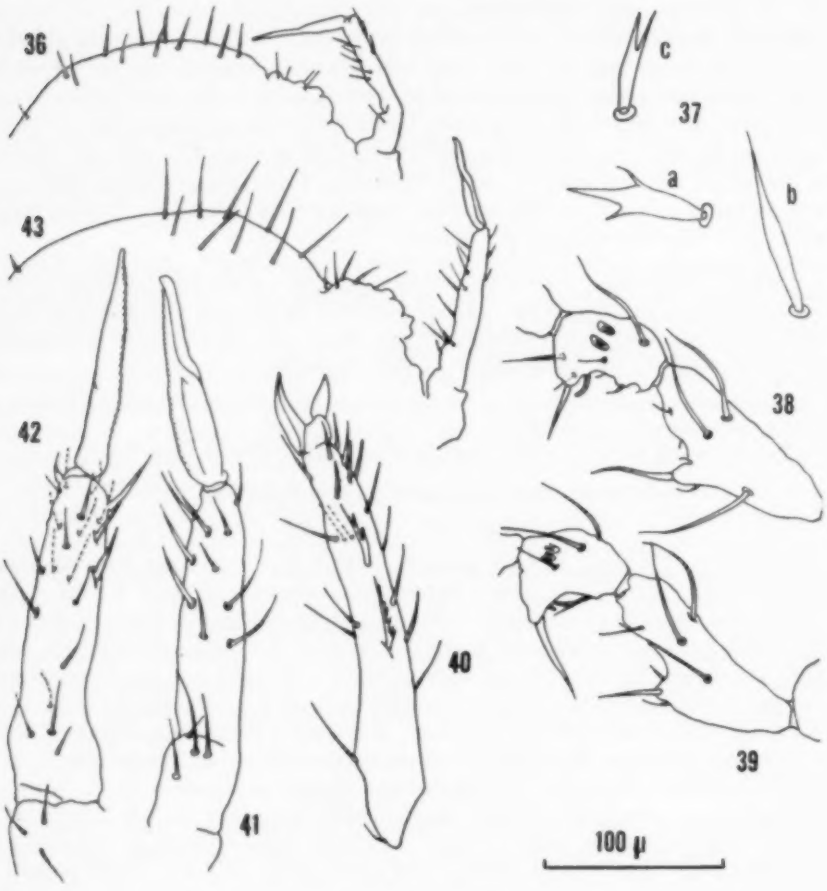
Material of this variety has been deposited in the British Museum (Nat. Hist.).

SMINTHURIDES (SPHAERIDIA) PROXIMA sp. n.

(Figs. 37, 38 and 40)

Female : 0·4 mm. Colour pinkish-violet. Body globular with thoracic segmentation almost obsolete. Anterodorsal setae small and forked, those further back simple but dilated. Thus on the mesonotal fold (very ill-defined) the medial setae are trifurcate, and 8·5 μ long, on the metanotal fold (fig. 38a) trifurcate and 10 μ long. The setae parallel with the most anterior bothriotrichium bifurcate (Fig. 38b–c) or simple but swollen and all short setae as far back as the long posterodorsals are distinctly dilated by comparison with the situation in *var. brevipila*. Posterodorsal setae up to 36 μ which is well over 3/4 length of mucro. Longest setae of genital segment 24 μ. No pregenital setae. Antenna 1·2 head diagonal with segments, 23, 36, 33 and 97 μ resp. Ant IV simple. Ant. III with small sensillae in separate but closely adjacent pits. Ant. I with anterior cleft not emarginate. 8+8 ocelli of which two are strongly reduced as in *brevipila*. Leg I with tibiotarsus, outer edge of claw and EA, 58, 18 and 20 μ resp., Leg II as 61, 17 and 17 μ, and leg III as 80, 18 and 10 μ. Claw I and II with one inner, one outer and a pair of lateral feet. Empodium with basal lamina 10 μ long and filament extending to 20 μ. Claw III with outer and lateral teeth and a very faint trace of inner tooth. EA with broad lamellae but filament almost completely obliterated. Tibiotarsus as in *S. serratus var. brevipila* with two strongly, unilaterally serrate appressed setae on the ventral side. Dens with three inner setae thickened,

but less strongly than in *var. brevipila* and with the outer distal seta simple and slender with no trace of the swollen base which characterizes *var. brevipila*. Otherwise the chaetotaxy is similar. The dens is 78 μ and the longest inner seta 18 μ. Mucro narrow, 43 μ long with serrate inner lamella and outer lamella smooth and sharply divergent in the proximal half. Tenaculum with



Figs. 36 to 43.—*Sminthurides serratus* and *S. proxima*.

Fig. 36.—*S. serratus var. brevipila* profile, × 1; 37, *S. proxima* anterodorsal setae, × 6·2; a, metanotal fold, near midline; b, next row back from a, near midline; c, next row back from b, level with anterior bothriotrichium, near midline; 38, *S. proxima* Ant. II : III of male, × 2·4; 39, *S. serratus var. brevipila* Ant. II : III of male, × 2·4; 40, *S. proxima* Tibiotarsus III, × 2·4; 41, *S. proxima* Dens and mucro, ventral view, × 2·4; 42, *S. serratus var. brevipila* Dens and mucro, ventral view, × 2·4; 43, *S. proxima* profile, × 1.

(All magnifications are relative to the scale included in the illustration.)

3 setae on the corpus, 3 teeth on the rami and with basal appendages. Ventral tube with 1+1 setae on the valves and 4+4 indistinct papillae are distinguishable.

Male : In the males and juveniles the thickened anterodorsal setae are not present, but the long posterodorsal setae are still striking. The male lacks metanotal vesicles and in the antennal clasping organ (Fig. 40) it has the proximal spine (i.e. of segment II) markedly the larger and stronger of the two.

Holotype female and allotype male (both mounted on slides) and one paratype male in alcohol have been deposited in the British Museum (Nat. Hist.).

Type locality : Organic, coprogenous soil under bushes in abandoned rice fields. Near riverine forest 2 Km. north of Jali, West Kiang. 18. viii. 57.

One adult female (Holotype), three adult males, two juvenile females.

SMINTHURIDES (*DENISIELLA*) *CF. RAMOSUS* Folsom 1932

Seasonal swamp in wooded savanna 1·5 Km. west of Jali (West Kiang) 10. viii. 57. approx. 50 individuals.

Temporary pools in road near Jali, 18. viii. 57.

This material, when adult, agrees in morphology of both sexes with the description given by Folsom and Mills 1938 excepting that the claw agrees with that of *sexpinnatus* Denis from Costa Rica in the possession of 3 to 4 lateral teeth and a basal fringed tunica. It should be noted that only in the fully adult female is the full length of the posterodorsal macrochaetae developed and almost fully grown subadults still have short setae. It seems possible that *sexpinnatus* Denis 1933 may therefore fall as a synonym of this species, thus simplifying the peculiar broken distribution at present known for *ramosus*. A slight difference from either form is that the male differs strikingly in coloration from the female. Female pale, greenish, while the male is blackish violet on the body with head and appendages pale.

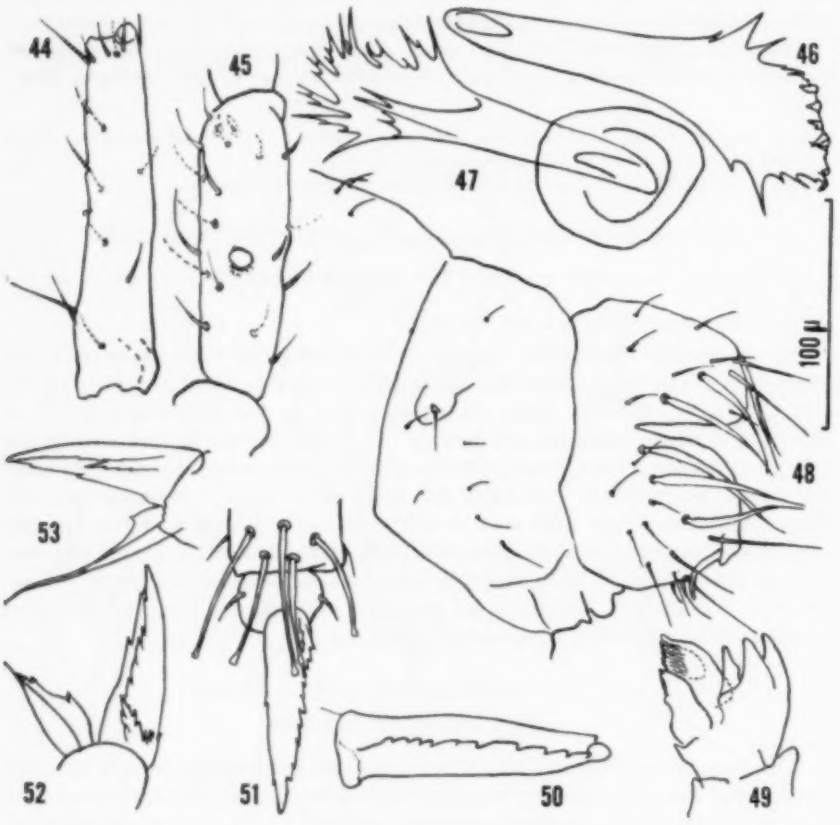
SMINTHURINUS STENOGNATHUS Börner

(Figs. 44 to 53 and 119)

This appears to be one of the commonest and most characteristic savanna species, and has been recorded in almost all the terrestrial soil types examined. Since in this genus the taxonomy is much confused by inadequate descriptions, the opportunity is taken to give here an extended redescription and illustrations.

Female : 0·9 mm. Coloration a strongly marbled pattern of blue-black pigment as in Fig. 119. Legs and antennae strongly banded. Furca pale. Body depressed, clothed with sparse, short, curving setae not more than 20 μ, less than half mucro. 3+3 bothriotrichia on furcal segment arranged as in *S. niger*. 1+1 short spinelike bothriotrichia on genital segment, which is separated by a suture from both furcal and anal segments. Perianal chaetotaxy as in Fig. 48. Subanal appendage 42 μ, well over half mucro, apically broadened and strongly fimbriated (Figs. 46 to 47). Antennae 1·56 head diagonal, with segments I to IV, 42, 87, 114 and 220 μ resp. Ant. IV with

eight rows of setae of which the longest are about 30 μ, and with an undivided, apical papilla. Ant. III with a simple, undivided proximal tubercle (rarely slight indication of division) and with sense organ of two short sense rods in separate cuticular pockets. Ocelli 8+8, of which the three inner corneae are the largest, all the others, including the central one of the group subequal,



Figs. 44 to 53.—*Sminthurinus stenognathus* Börner.

Fig. 44.—Dens, × 1·4 ; 45, Ant. III , × 1·4 ; 46, Subanal appendage, × 4·8 ; 47, Subanal appendage, × 4·8 ; 48, Anal and genital segments, × 1 ; 49, Capitulum of maxilla, × 2·4 ; 50, Mucro, × 2·4 ; 51, Claw II, dorsal view, × 2·4 ; 52, Claw III, lateral view, × 2·4 ; 53, Claw I, lateral view, × 2·4.
(All magnifications quoted are relative to the scale included in the illustration.)

slightly smaller. Legs with 4, 5, 5 clavate setae subapically on tibiotarsus, the arrangement on II and III being as in Fig. 51. On leg I, the most anterior of the distal pair is that missing. Claws on all feet with two inner teeth, a few teeth on the anterior lateral lamella and many teeth on the posterior

lateral lamella. Furthermore, there is a strongly toothed, posterior pseudonychium which is longest (1/2 claw) on leg I. EA on leg I (Fig. 53) with one inner tooth and with long apical filament which exceeds inner edge of claw. EA of leg II similar to that of leg III (Fig. 52) with larger lamella bearing two inner teeth and traces of subapical denticulation, and with very short filament. Tibiotarsus, claw (outer edge) and EA on leg I, 163, 42 and 40 μ resp., on leg II, 160, 40 and 23 μ resp., and on leg III, 228, 45 and 23 μ resp. Trochanteral organ present on leg III as a small sense spine in a trichobothrium. Furca with long manubrium and dens with chaetotaxy as in Fig. 44, having only 1+1 ventral setae apart from the apical whorl (*c.f. salti* Del. in which there are 2+2. Mucro 57 μ, less than half dens (137 μ on ventral edge), with inner lamella having 10 to 12 strong teeth and outer lamella smooth except for a single small tooth in which it ends just short of the apex. No ventral lamella or mucronal seta. Tenaculum with 3+3 teeth on rami, 1+1 basal, clavate appendages, low pars posterior and high pars anterior bearing a single seta at apex. Ventral tube without setae on base and with smooth vesicles. Capitulum of maxilla (Fig. 49) with short lamellae.

Male : 0·55 mm. Apart from the small size, little trace of sexual dimorphism. In the perianal chaetotaxy the setae are not so strongly flattened, the median dorsal seta is not bifid as in the female, and the subanal appendage is replaced by a curved seta, directed backwards.

Note : It will be noted that the proportions of Antenna to Head diagonal are not a valid character for recognizing the species. One other discrepancy from the original description is the size of the ocelli. Since descriptions here refer to the cuticular cornea and Börner may have referred to the appearance of the internal lenses, the difference is not in my opinion significant.

Localities : Examples are only given since the species is very widely distributed.

Keneba, Gambia, 8. viii. 57. Litter from wooded savanna 1 Km. east of Keneba.
Jali, Gambia, 18. viii. 57. Dark coprogenous soil in gallery forest.
Keneba, Gambia, 2. ix. 57. Cultivated soil near village.

BOURLETIELLA sensu lat.

Gisin (1946 and 1957) sets out the reasons for retaining this as a single genus at the present early stage of knowledge. His thesis is fully supported by the present worker and in this paper his practice is adopted and extended to the material described here. Thus it is my opinion that at present, ease of determination is best served by regarding species that might be referred to *Prorastriopes* as part of the *Deuterosminthurus* group of *Bourletiella* and keying them out as such. Furthermore, since *Bourletiella gisiniana* sp. n. has certain characteristics linking *Rastriopes* to *Bourletiella* s. str., I do not see that the former can be accorded more than subgeneric rank. On the other hand, *Bovicornia* seems to be so well separated that its generic status should be upheld, and it is so treated here.

All the species here referred to as *Bourletiella* (*Deuterosminthurus*) agree in having some stronger spines arranged irregularly on the inner side of the

tibiotarsus. These are similar to those found in *Bovicornia* and some of them have a characteristic slightly curved tip due to a minute unilateral subapical lamella. This is presumably the " primitive rastral organ " by which *Prorastriopes* is recognized, but the spines are not greatly different from those found in the same position in *Bourletiella* s. str. and European *Deuterosminthurus*. This is certainly true of *Bovicornia* and therefore presumably of Prorastriopes, although since neither *P. pulchra* or *P. risbeci* have yet been encountered it cannot be regarded as completely settled. Judging by Delamare's figure 2c (1947 page 105), *Prorastriopes* agrees with *Bovicornia* in having 3 clavate tenent hairs on leg III.

In the following descriptions close attention is paid to the important details of the perianal chaetotaxy and the nomenclature introduced by Gisin (1946 page 250) is followed throughout.

BOURLETIELLA (*DEUTEROSMINTHURUS*) *SPATHACEA* Börner 1907

One adult female agreeing in all particulars with the original description.

Keneba, Gambia, 12. xi. 57. Swept from groundnut vegetation in farms.

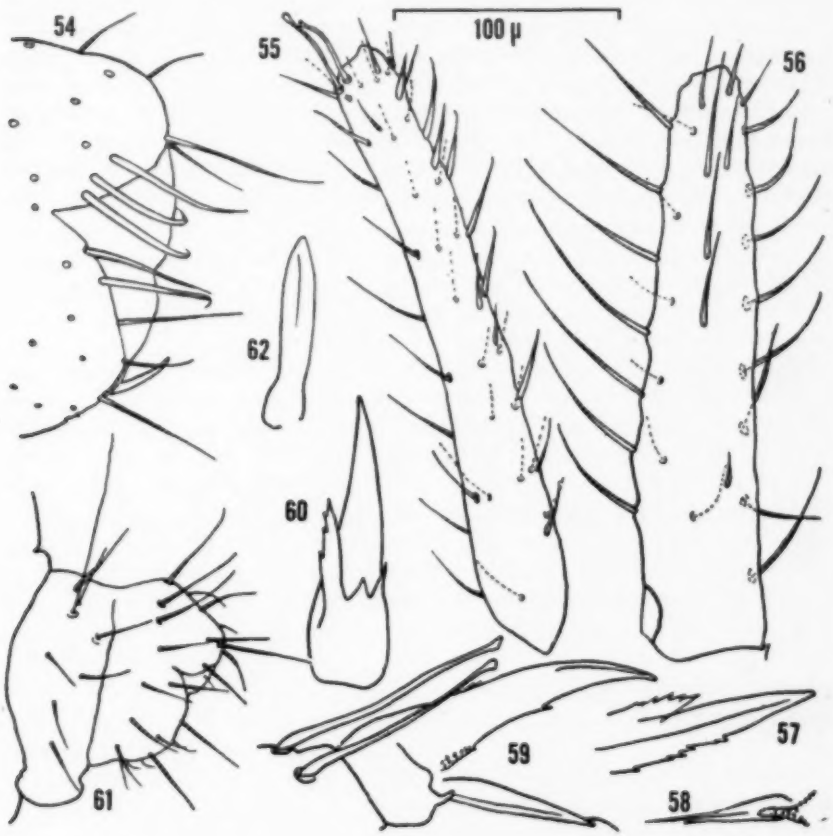
BOURLETIELLA (DEUTEROSMINTHURUS) ALATIPES sp. n.

(Figs. 54 to 63 and 121)

Female : Length 1·05 mm. Coloration yellow with a strongly marked superficial pattern of blue-black pigment as in Fig. 121. Legs and furca pale. Antennae violet. Body clothed with simple smooth setae, of which the longest posterodorsal setae are 68 μ, and median anterodorsal setae 27 μ. Bothriotrichia 3 +3 in a lateral diagonal line on furcal segment, 2 +2 on genital segment. Integument finely granulate. Antennae 1·7 head diagonal with segments I to IV 53, 125, 167 and 308 μ, resp. Antenna IV with seven subsegments which from base to apex measured 84, 37, 35, 33, 33 and 51 μ resp. Antenna II and III without outstanding macrochaetae. Ocelli 8 +8 of which the corneae of the median (C) and the posterior (F) are markedly smaller than the others. Leg I ,with tibiotarsus outer edge of claw and EA, 209, 57 and 30 μ, leg II, 213, 53 and 27 and leg III, 270, 57 and 34 μ resp. Tenent hairs 3, 3 and 2. The spines on the inner face of the tibiotarsus are strong and sometimes slightly curved at apex, but no subapical lamella could be seen. Claws (Figs. 57, 59 and 60) similar on all feet, with a variable number of teeth on the anterior lateral lamella and with a basal fringe (? very closely applied tunica) which subtends on the posterior side a long pseudonychium. This feature is extremely difficult to detect, especially on leg III where it is very closely applied to the side of the claw. EA with narrow lamina and moderately long, subapical filament on leg I (Fig. 58), longer lamina but still subapical filament on II and III. Chaetotaxy of tarsus III as in Fig. 55. Manubrium with 7 dorsal setae. Dens 262 μ, with chaetotaxy as Fig. 56. Inner and outer lateral setae very elongate, the most distal of the inner row 65 μ, the longest 80 μ or 2/3 mucro. Mucro typical with three entire lamellae and no mucronal seta ; 110 μ. Tenaculum with 3 +3 teeth on rami and high corpus bearing 3 apical setae. Ventral tube with no setae on base and with long, tuberculate vesicles.

Perianal chaetotaxy as in Fig. 54. Setae IV, V, VI, VII and VIII are strongly thickened (but not flattened) and curved inwards. Subanal appendages (Fig. 62) very short, 30 μ and thickened on the outer side.

Male : Length 0·6 mm. Antennae 1·9 head diagonal. Perianal chaetotaxy as Fig. 61. Otherwise as female.



Figs. 54 to 62.—*Bourletiella alatipes.*

Fig. 54.—Anogenital segment of female (Holotype), × 1 ; 55, Tibiotarsus III (Holotype), × 1 ; 56, Dens (Holotype), × 1 ; 57, Claw III, dorsal view, × 2·4 ; 58, Empodial appendage of leg I, × 2·4 ; 59, Claw III, lateral view, × 2·4 ; 60, Claw II, oblique dorsal view, × 2·4 ; 61, Male anogenital segment, × 1 ; 62, Female subanal appendage, × 2·4.
(All magnifications quoted are relative to the scale included in the illustration.)

Types : Holotype female, allotype male, paratypes in alcohol and further paratypes on slides have been deposited in the British Museum (Nat. Hist.). Further paratypes in author's collection.

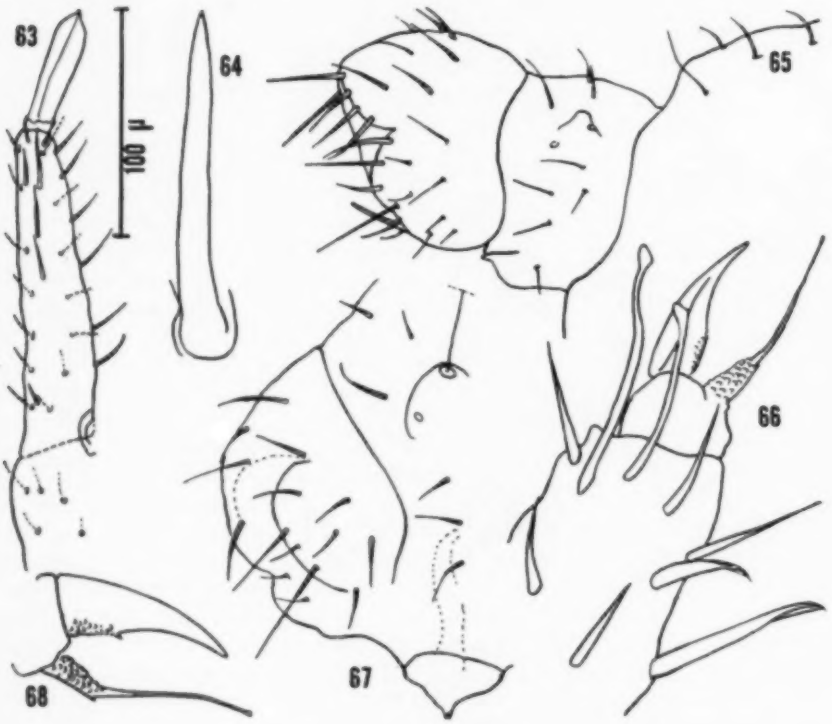
Type locality : Keneba, Gambia, 10. viii. 57. Swept from vegetation of seasonal swamp in the savanna.

Also recorded from Basse, Gambia, 18. ix. 57. Seasonal swamp in the Sabbi Forest Reserve.

BOURLETIELLA (DEUTEROSMINTHURUS) SAVANNA sp. n.

(Figs. 63 to 68 and 120)

Female : 0·73 mm. Coloration brown, with superficial pigmentation as in Fig. 120, comprising a broad saddle-like mark posterodorsally on the furcal segment and smaller patches laterally, and on the head and anogenital segment. Clothing of short curving setae most of the posterodorsal group being not more than 19 μ. On each side, the most posterior seta of the medial row is markedly longer than the others, 27 μ. (These are the setae normally measured.) Bothriotrichia 3+3 on the furcal segment, equidistant and on a diagonal line ; 2+2 on genital segment in small trichobothria. Antennae 1·5 head



Figs. 63 to 68.—*Bourletiella savanna.*

Fig. 63.—Dens and mucro (Holotype), × 1 ; 64, Subanal appendage (Holotype), × 4·8; 65, Anogenital segment of female (Holotype), × 1 ; 66, Claw III and apex of tibiotarsus (Holotype), × 4·8 ; 67, Anogenital segment of male, × 2·4 ; 68, Claw I, lateral view (Holotype), × 4·8.

(All magnifications quoted are relative to the scale included in the illustration.)

diagonal with segments I to IV, 30, 65, 80 and 179 μ resp. Antenna IV with 7 subsegments of which the basal is twice as long as the others. Ant. II and III without outstanding macrochaetae. S.O. Ant. III with two sensillae in a common fossa and a supplementary sensilla a little to one side. Ocelli 8+8 of which C and F are smaller than the others. Leg I with tibiotarsus, claw and EA, 141, 19 and 19 μ resp., leg II, 148, 19 and 19 μ resp., and leg III, 198, 19 and 19 μ resp. Tibiotarsi with 3, 3, 2 tenent hairs and with a number of strong spines on the inner side arranged " without order ", which are slightly lamellate subapically. Claws I (Fig. 74) to III (Fig. 72) similar, with a pair of outer teeth at approx. 0·7 from the base and without a true inner tooth. However the proximal part of the inner edge is granulate and the most distal granule projects tooth-like, especially on Claw I. Empodial appendage with a granulate base, a much reduced lamina lying appressed to this base and the apex of which is barely visible as a tooth lying behind the elongate, tapering and apically minutely clavate filament. Manubrium with 5 dorsal setae. Dens with chaetotaxy as in Fig. 63, having 4+2 in the inner lateral row. Dens 144 μ. Mucro 57 μ, with three, simple entire lamellae of which the ventral reaches the apex. Dorsodistal seta 19 μ. Tenaculum with 3+3 teeth on rami and 3 setae on the corpus. Ventral tube without setae and with long strongly tuberculate vesicles. Perianal chaetotaxy as in Fig. 65, unusually short. Seta V on the lower valve and VI and VII on the upper valve thickened and incurved, II and IV on the lower. VIII and IX on the upper being straight strong macrochaetae. I is short and curved. Subanal appendage (Fig. 64) 35 μ, curved and spine-like.

Male : 0·5 mm. with antennae 1·55. Head diagonal. Perianal chaetotaxy as in Fig. 67. (This is drawn from a specimen mounted in P.V.A. which is not well orientated, the upper valve being seen in posterior view. The dotted line indicates the line of the perianal chaetotaxy and terminates at the median unpaired seta.) The chaetotaxy is complete but shorter than usual. Otherwise as female.

Types : Holotype female in alcohol and allotype male mounted, together with a number of immature specimens in alcohol have been deposited in the British Museum (Nat. Hist.).

Type locality : Keneba, Gambia, 6. viii. 56. Swept from bushes in the open savanna.

Note : This species has claw and empodial appendage very similar to those of *Bovicornia* in having no true inner tooth but instead a denticle formed by the most distal granule of the base of the claw and no true lamina on the EA. It therefore agrees in this particular with *Prorastriopes* Delamare, but differs from the two described species in size of subanal appendage and in its very different coloration.

BOURLETIELLA (DEUTEROSMINTHURUS) VIOLACEA sp. n.

(Figs. 69 to 77)

Female : 0·64 mm. Coloration violet-blue which is darkest on the postero-dorsal region and flanks, paler anteriorly and on the anogenital region. Legs, furca and venter pale. Antennae violet. Clothing of smooth curved setae

of which the longest posterodorsals are 30 μ. Bothriotrichia of furcal segment 3+3 equidistant on a diagonal, lateral line. Genital segment with 2+2, both in very large trichobothria. Antennae 1·7 head diagonal with segs. I to IV, 35, 57, 91, and 190 μ resp. Ant. IV with 7 subsegments of which the basal is approx. twice, and the apical 1·5 the intermediate segs. Ant. II and III without outstanding macrochaetae. S. O. Ant. III with two sensillae in a common fossa and a supplementary sensilla also in a shallow fossa on the outer side. Ocelli 8+8 of which C and F are distinctly smaller. Leg I with tibiotarsus, outer edge of claw and EA 133, 15 and 15 μ, leg II 133, 15 and 15 μ

Figs. 69 to 77.—*Bourletiella violacea.*

Fig. 69.—Dens, × 1 ; 70, Mucro, × 1·7 ; 71, Anal segment, × 1·7 ; 72, Claw III, lateral view, × 3·4 ; 73, Claw III, dorsal view, × 3·4 ; 74, Claw I, lateral view, × 3·4 ; 75, Spine from inner side of tibiotarsus, × 3·4 ; 76, Anogenital segment of male, × 1·7 ; 77, Subanal appendage of female (Holotype), × 3·4.
(All magnifications quoted are relative to the scale included in the illustration.)

and leg III, 171, 17 and 15 μ resp. (Owing to the shape of the EA it cannot be accurately measured.) Tenent hairs 3, 3 and 2 and all tibiotarsi bear some slightly thickened spines which are slightly lamellate at the tip. Claw I (Fig. 74) with one inner tooth and one pair of lateral teeth. Claw II and Claw III (Figs. 72 and 73) with lateral but no inner teeth. EA similar on

all legs, with short, granulate base and long, strongly recurved filament. Manubrium with 5 dorsal setae. Dens 156 μ, very long in proportion to mucro (more than 3·5), with chaetotaxy as in Fig. 69. Inner lateral row very strongly reduced, with only two setae distally and two basal. Dorsodistal seta 18 μ, about 2/5 mucro. Mucro 42 μ, with strong basal, transverse crest, three lamellae and no mucronal seta. The ventral lamella (in contrast to most species of the group) does not reach the apex which therefore looks smoothly rounded in dorsal view (Fig. 70). Tenaculum with 3+3 teeth on rami and high corpus with three apical setae. Ventral tube without setae on base and with long, tuberculate vesicles. Perianal chaetotaxy as in Fig. 71, incomplete. Which seta are absent is not completely certain, but my interpretation is as follows. I obsolete, II and IV long and straight, III and V thickened and strongly incurved, on the lower valve. On the upper valve, VI and VIII thickened and incurved, IX and the median unpaired seta are long, straight macrochaetae and VII (?) obsolete. The subanal appendage is 27 μ, simple and spine-like (Fig. 77).

Male : 0·5 mm. Antennae 1·9 head diagonal. Chaetotaxy of anal segment as Fig. 76. Coloration and anatomy otherwise as in female. No differentiated occipital organ or specialized sexual features.

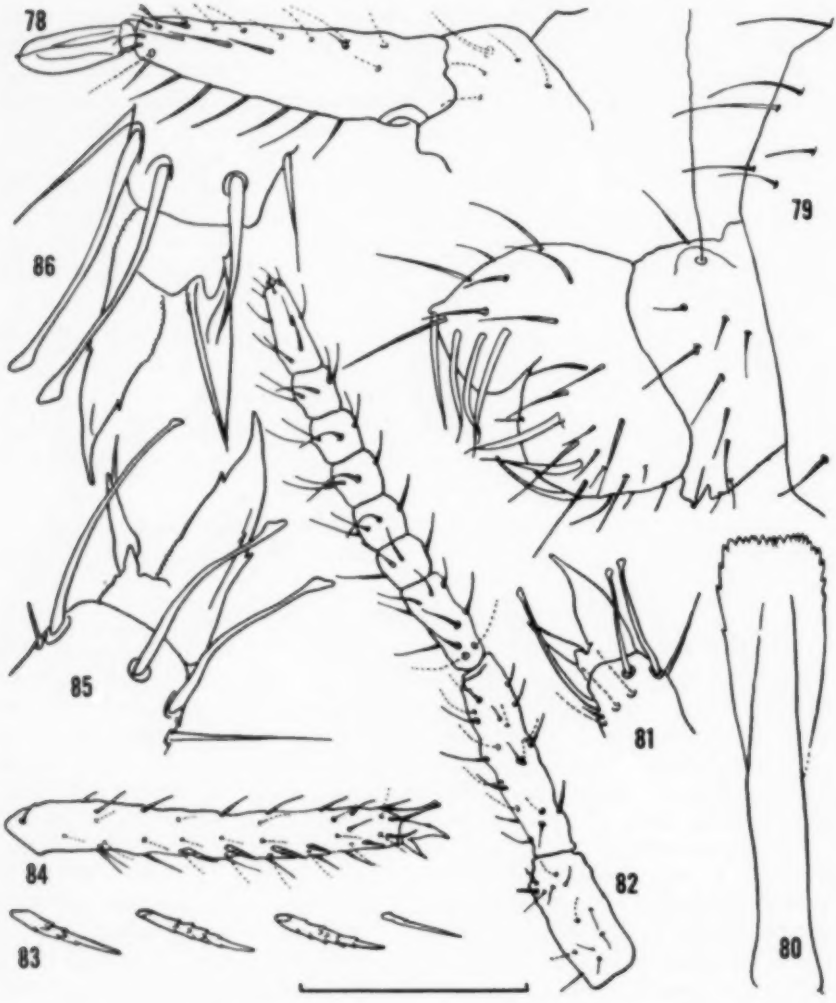
Types : Holotype female, allotype male and paratypes in alcohol, and further paratypes on slides have been deposited in the British Museum (Nat. Hist.). Further paratypes in author's collection.

Type locality : Keneba, Gambia, 29. xi. 57. Swept from flowering vegetation of dried out temporary swamp in the savanna 3 Km. east of Keneba. This is also the type locality of *B. alatipes*.

BOURLETIELLA (RASTRIOPES) GISINIANA sp. n.

Female : length 0·67 mm. Coloration typical of the subgenus, with deep violet-black body and legs and appendages pale (Fig. 122). Laterally two stripes of blue pigmentation stretch forward across the neck and onto the head, the upper including the eye patch, the lower one shorter extending on to the gular region. Anogenital segment pale. Body clothed with simple smooth setae of which the posterodorsal are much the longer. Longest posterodorsal setae 46 μ, anterodorsals 14 μ. Bothriotrichia 3+3, smooth and lying equidistantly along a diagonal, lateral line on the furcal segment, 2+2 on a high prominence on the genital segment. Integument finely granulate throughout. Antennae (Fig. 82) 1·5 head diagonal with segments I to IV, 38, 65, 87 and 190 μ respectively. Antenna IV with 7 subsegments of which the apical and basal are twice the length of the intermediate segs. The basal subsegment lacks the pair of short sensillae noted in *amphigya* and *tricuspidata* by Börner. Antenna III without outstanding macrochaetae and with sense organ consisting of two rods in a common fossa. Ocelli 8+8 of which the median and the posterior (C and F on standard nomenclature) are very much smaller than the others (this refers to corneae as seen in lateral view). Leg I with tibiotarsus, outer edge of claw and EA, 141, 23 and 15 μ, Leg II 144, 23, and 15 μ, and Leg III 171, 23 and 15 μ resp. Leg III carries

on the inner side of the tibiotarsus a typical " rastral organ " (Figs. 83 and 84) of four large, serrate spines. No such serrate spines occur on fore or mid tarsi. There are 3, 3 and 2 normal, *Bourletiella* type tenent hairs. Claws similar on all feet and sharply narrowed in the distal third. This is due to



Figs. 78 to 86.—*Bourletiella* (*Rastriopes*) *gisiniana*.

Fig. 78.—Dens and mucro, × 1 ; 79, Anogenital segment of female (Holotype), × 1 ; 80, subanal appendage, × 4·8 ; 81, Claw II, lateral view, × 2·4 ; 82, Antenna (Holotype), × 1 ; 83, " Rastral Organ " of tibiotarsus, × 3·0 ; 84, Tibiotarsus III, × 1 ; 85, Claw III, lateral view, × 4·8 ; 86, Claw I, lateral view, × 4·8.

(All magnifications quoted are relative to the 100μ scale included in the illustration.)

the very wide lateral lamellae which extend only up to this point and do not reach the apex. 1+1 strong, lateral teeth and one strong inner tooth. EA of foot I with narrow lamina and strong subapical seta. On II and III the lamina is wider and the filament apical and almost obsolete. There is no differentiated trochanteral organ. Dens with chaetotaxy as in Fig. 78, 137 μ long (ventral edge). Mucro typical of the family, with three entire lamellae and without mucronal seta ; length 57 μ. Tenaculum with 3+3 teeth on rami and high corpus with three apical setae. Ventral tube without setae on base and with long vesicles bearing 8 rows of very strong tubercles. Perianal chaetotaxy as in Fig. 79, with macrochaetae II and IV on the lower valve and VI, VII, VIII and the unpaired median seta of the dorsal valve, all strongly curved, flattened lamella-like and serrated along the edges. Subanal appendages 46 μ, (four-fifths mucro) flattened and apically serrate (Fig. 80).

Male : 0·55 mm. Coloration as female. Antennae 1·7 head diagonal. Perianal chaetotaxy unmodified with no special characteristics. No occipital organ or dorsal clasping organ. In the three specimens examined by me, the rastral organ of tarsus III consisted of two serrate spines only. Other details agree with the female.

Types : Female holotype, male cotype and a series of paratypes, all in alcohol have been deposited in the British Museum (Nat. Hist.). Further paratypes in author's collection.

Type locality : Keneba, Gambia, 9. vi. 56. Swept from moist vegetation in rice fields 3 Km. west of Keneba. Twenty specimens.

Also recorded 13. vii. 56, in a similar situation, 2 Km. west of Keneba.

Affinities : This species, while having the characteristic " rastral organ " of the subgenus well developed, is quite distinct from all others so far described, in its small size, the small number of subsegments in Ant. IV, a characteristic making it transitional to the other subgenera of *Bourletiella* lat., and in its unique perianal chaetotaxy.

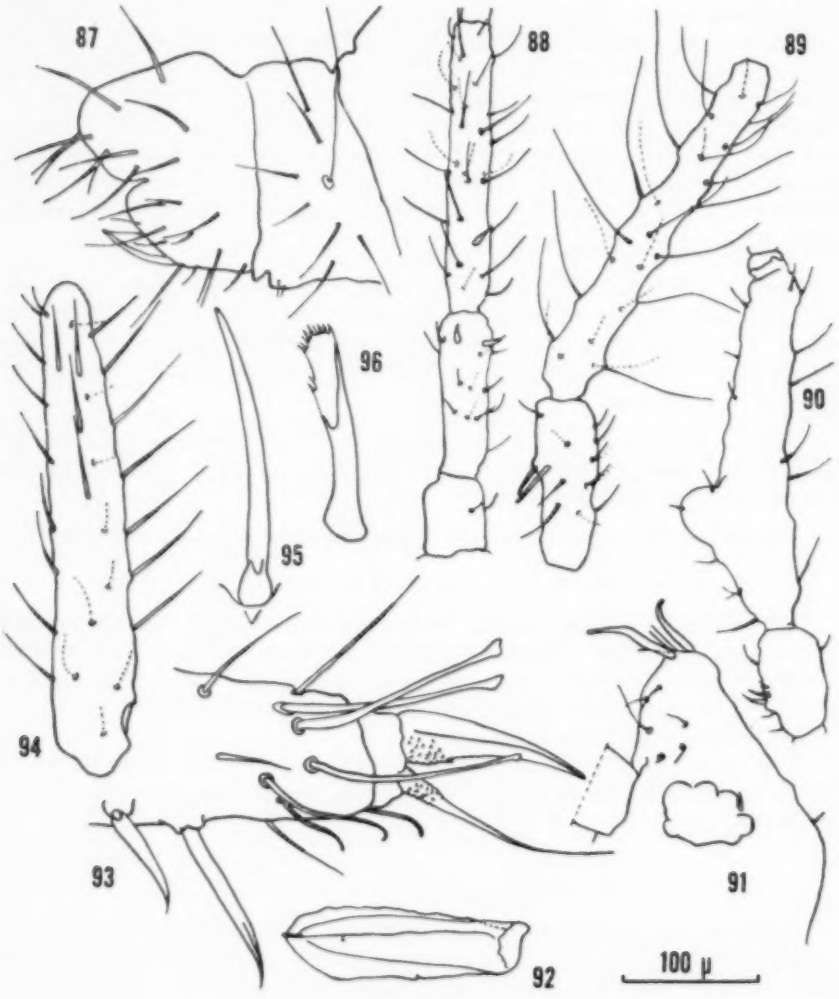
It gives me great pleasure to dedicate this species to the Swiss specialist, Dr H. Gisin, to whose advice and help I owe most of my knowledge of the Collembola.

BOVICORNIA Delamare Debouteville

This genus is highly distinctive, not only in the nature of its sexual dimorphism but also in the nature of the perianal chaetotaxy, the presence of 1+1 setae on the ventral tube and the tibiotarsal chaetotaxy. The latter is characterized by 3, 3 and 3 tenent hairs in the normal position and the presence on the inner side of characteristic flexed tenent hairs. Since the type species was described from Senegal, it is not surprising that it should be recorded from the Gambia. In the latter area, however, the genus is also represented by a second, very distinct form which is described here under the name *Bovicornia uniformis* sp. n.

BOVICORNIA CORONATA Delamare 1947
(Figs. 90 and 96)

As certain details have been used to distinguish this species from *B. uniformis* sp. n. which were not mentioned in the original description, this has



Figs. 87–96.—*Bovicornia uniformis* and *B. coronata*.

Fig. 87.—*B. uniformis* Anogenital segment of female, × 1 ; 88, *B. uniformis* Female antenna I to III (Holotype), ×1·3 ; 89, *B. uniformis* Male antenna II to III, × 1 ; 90, *B. coronata* Male antenna II to III, × 1 ; 91, *B. uniformis* Male vertex, lateral view, × 1 ; 92, *B. uniformis* Mucro, × 1·7 ; 93, Claw III, × 4·0 ; 94, Dens, × 1 ; 95, *B. uniformis* Subanal appendage, × 3·4 ; 96, *B. coronata* Subanal appendage, × 4·0.
(All magnifications quoted are relative to the scale included in the illustration.)

been supplemented by illustrations of the male antennal segs. II and III and of the female subanal appendage (Figs. 90 and 95). *B. coronata* is a very widely distributed form in the Gambia where it has been collected by sweeping short herbaceous vegetation throughout the savanna during the early rains and from agricultural land (e.g. groundnuts) throughout the rains. Rare in the full-grown tall-grass at end of the rainy season.

Keneba, 6. viii. 56. Swept from short grass in compound of Medical Research Council field station.

Keneba, 10. viii. 57. Wooded savanna 3 Km. east of Keneba, swept from short herbaceous vegetation edging temporary "bush" swamp.

BOVICORNIA UNIFORMIS sp. n.

(Figs. 87 to 89, and 91 to 95)

Female : 1·1 mm. Colour uniformly greenish-blue or with slightly augmented blue pigment laterally. Body clothed with simple smooth setae. Posterodorsal setae 84 μ slightly less than mucro. 3+3 simple, smooth bothriotrichia lying equidistantly on a diagonal line laterally on furcal segment. 2+2 bothriotrichia on genital segment. The perianal chaetotaxy (Fig. 87) has been checked against *B. coronata* and agrees throughout excepting in shape of subanal appendage. This is a long, simple curving spine (Fig. 95) 61 μ or 2/3 mucro, whereas in *coronata* it is flattened and fimbriate at the apex (Fig. 96), and approx. half mucro. The three forked setae on the upper anal valve are present. Antennae 2·28 head diagonal with segs. I to IV 57, 118, 213 and 391 μ resp. Ant. IV divided into seven subsegments of which the basal is more than two times the others. Antenna II and III (Fig. 88) markedly different from *coronata* in the presence of two apical spines on seg. II and one sub-basal spine on seg. III. S. O. Ant. III with two minute sensillae in a common fossa. Ocelli 8+8 of which the median and posterior are only slightly smaller than the others, situated on black eye-patches. Leg I with tibiotarsus outer edge of claw and EA 266, 38 and 35 μ resp. Claw and EA similar on all feet. Strong spines on inner side of tibiotarsus present on all legs (as in *coronata*) consisting of a distal group as illustrated by Delamare. There are two similar spines situated further back on the inner edge of the tibiotarsus. Some are subapically lamellate. Leg III with tibiotarsus, claw and EA, 304 38 and 38 μ resp. Claw as in Fig. 93, with three dorsal clavate hairs, and three ventral flexed setae. The claw has no lateral teeth, a very small inner tooth, or tooth-like projection distal to the papillate base (present in *coronata* also) and the EA is simple, tapered and acuminate. No differentiated trochanteral organ. Dens with chaetotaxy (ventral) as in Fig. 94. In my experience, this is true also of *coronata*, both forms lacking the proximal ventral setae illustrated by Delamare and having the distal seta paired. (It is possible that Delamare drew the same setae as both ventral and dorsal in the basal part of his figure, 1b). Dens 266 μ with apical seta of inner lateral row 60 μ, subapical 76 μ. Mucro (Fig. 92) of typical Bourletiella type, without mucronal seta, 91 μ long. Tenaculum with 3+3 teeth on rami and high corpus having 3 apical setae. Ventral tube with 1+1 strong curved setae on valves and with long, strongly tuberculate vesicles.

Male : 0·75 mm. Coloured as female. Vertex (Fig. 91) conical with two strong, curved, blunt spines 72 μ long (mucro 68 μ) characteristic of the genus and three median setae. The lateral eversible vesicles are almost obsolete, much less marked than in *coronata*. Antennae very different to those of *coronata* (*cf.* Figs. 89 and 90). Antenna II with two long blunt spines on inner side (in *coronata* this segment has a very large basal lobe bearing a minute seta as this tip and the clothing consists of relatively short setae. It may be noted that in Fig. 90 only the marginal chaetotaxy is drawn as the intense pigmentation of the antennae in this species prevented the complete chaetotaxy being seen.) Male antennae 3·5 head diagonal (measured from occiput to clypeus) with segments 91, 129, 274 and 445 μ resp. Ant. IV with 7 subsegments, 163, 53, 49, 46, 43, 38 and 53 μ resp. Posterodorsal setae longer than mucro (90 μ). Perianal chaetotaxy much shorter than in female, and lacking the bifid setae.

Types : Holotype female and allotype male, in alcohol, together with a series of paratypes both in alcohol and mounted on slides, have been deposited in the British Museum (Nat. Hist.).

Type locality : Keneba, Gambia, 6. viii. 56. Swept from grass in the grounds of the Medical Research Council field station.

SPYROTHECA CF. MULTIFASCIATA (Reuter 1878)

One adult male and one immature female of a species of *Sphyrotheca* having most key characters in common with the above. Certain features suggest, however, that when material of the adult female is forthcoming this will prove to be a distinct species.

Keneba, Gambia, 2. x. 57. Sandy soil under dense herbaceous vegetation. Fallow groundnut farm near M.R.C. field station.

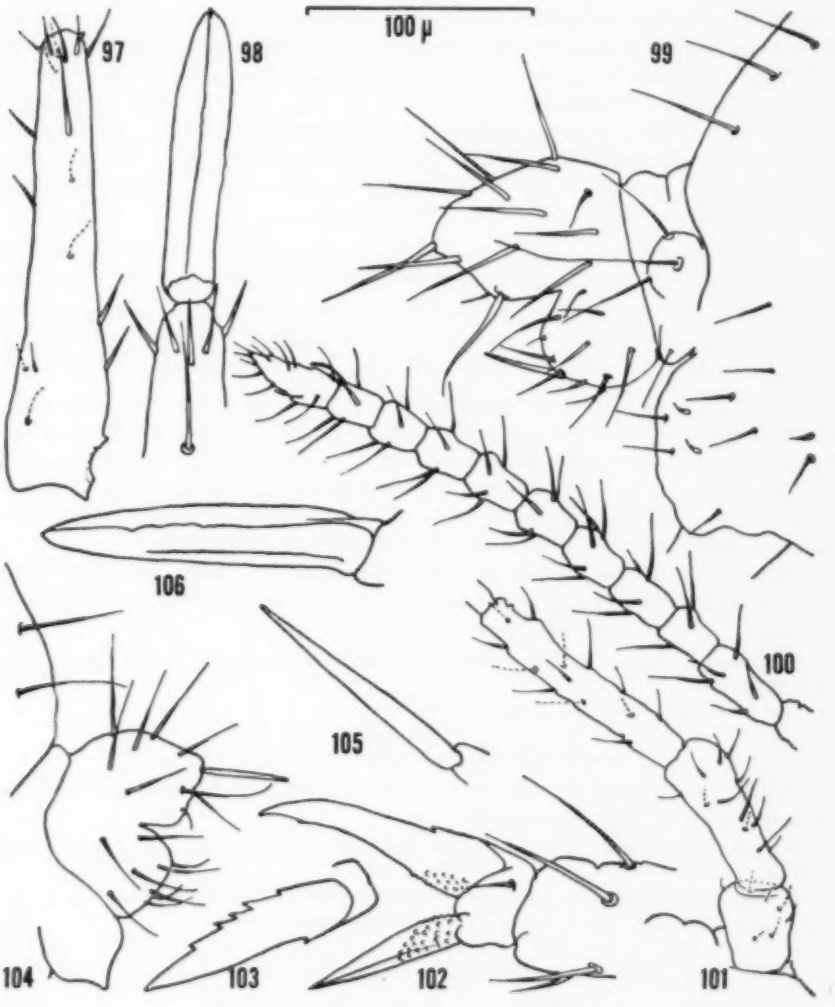
4. ix. 57. Swamps 3 Km. west of Keneba.

SMINTHURUS STYLIFER sp. n.

(Figs. 97 to 106 and 133)

Female : Up to 0·64 mm. (measured individual 0·62 mm.). Coloration (Fig. 123) black, with pale area mid-dorsally ; head and appendages pale, antennae lightly pigmented violet. Body clothed with simple, smooth setae. Posterodorsal setae 42 μ, approx. two thirds mucro. Furcal segment with 3+3 simple non-ciliated bothriotrichia but also bearing two long setae not arising from enlarged trichobothria. Integument finely granulate throughout. Occipital chaetotaxy of simple, fine hairs in both sexes. Antennae slightly less than twice head diag., with segments I to IV (Figs. 100 and 101) 34, 72, 95, and 281 μ, resp. Antenna IV with ten subsegments, of which the apical is conical, without outstanding macrochaetae. S.O. Ant. III with 2 clubs in a circular depression. 6+6 large corneae situated on a black eyepatch, no trace of supplementary microcorneae ; no trace of postantennal organ. Claw similar on all legs, with anterior lateral lamella bearing a single basal tooth, posterior lateral lamella bearing a single basal tooth, posterior lateral lamella

bearing 5 or 6 serrations. Inner lamella with a single subapical tooth. Empodial appendage three winged, acuminate, more than 3/4 inner edge of claw. Tenent hairs absent. Tibiotarsus, outer edge of claw and EA 175,



Figs. 97 to 106.—*Sminthurus stylifer*.

Fig. 97.—Dens, × 1·3 ; 98, Mucro (Holotype), × 2·0 ; 99, Anogenital segment of female (Holotype), × 1 ; 100, Antenna IV (Holotype), × 1 ; 101, Antenna I, II and III (Holotype), × 1 ; 102, Claw III, lateral view (Holotype), × 4·8; 103, Claw III, dorsal view (Holotype), × 4·8 ; 104, Anogenital segment of male, × 1·3 ; 105, Subanal appendage of female, × 3·1 ; 106, Mucro, lateral view, × 2·4.

(All magnifications quoted are relative to the scale included in the text.)

23 and 15 μ on leg I, 179, 23 and 15 μ on leg II and 228, 24 and 16 μ on leg III. Trochanteral organ present on leg III consisting of a single, strong, curved spine. Dens 180 μ (ventral side) with chaetotaxy very reduced (Fig. 97) apically with a whorl of six short setae and ventrally (Fig. 98) with an additional long, strong subapical seta. Mucro 64 μ, with all three lamellae smooth, entire and reaching apex. (Figs. 98 and 106). Mucronal seta absent. Laterally, furcal segment bears 3+3 short, curved, smooth spines at base of manubrium (Fig. 99). Perianal chaetotaxy as in Fig. 99. Subanal appendage (Fig. 105) a simple, smooth spine 42 μ or 2/3 length of mucro. Tenaculum with 3+3 teeth on rami and high corpus bearing 2 apical setae. Ventral tube with 1+1 setae situated anteriorly on valves, no setae on base and with strongly tuberculate vesicles.

Male : Agrees with female in most particulars. Size 0·50 mm. Antennae 2·3 head diagonal with segs. I to IV 27, 56, 61 and 224 μ resp. Perianal chaetotaxy as Fig. 104, with median unpaired seta modified into an elongate, cigar-shaped style (from which the species is named) which is 30 μ long or 3/5 mucro (53 μ). Furcal segment with 3+3 lateral spines as in female.

Affinities : Clearly falls within the genus *Sminthurus* sensu lat., but has little in common with the genus in the narrow (and I believe correct) sense employed by Stach (1956), since it lacks PAO and macrochaetae of Ant. III. No doubt the genus will be fragmented when the species are better known but in my opinion, the time is not yet ripe. In Stach (1956) this species keys out in the vicinity of *S. wahlgreni* with which it has little in common.

Types : Holotype female and allotype male in alcohol, together with paratypes in alcohol and mounted on slides, have been deposited in the British Museum.

Type locality : Keneba, Gambia, 8. viii. 57. Litter from wooded high-grass savanna 1 Km. east of Keneba.

Also known from cultivated soils near Keneba.

SMINTHURUS MACROCEROS Denis 1933

Widely distributed in litter and under logs, etc., throughout the savanna and the derived agricultural land.

E.g. Keneba, Gambia, 31. vii. 56. Under stones and wood in compound of M.R.C. Field Station.

Keneba, Gambia, 8. viii. 57. Litter in wooded savanna 1 Km. east of Keneba.

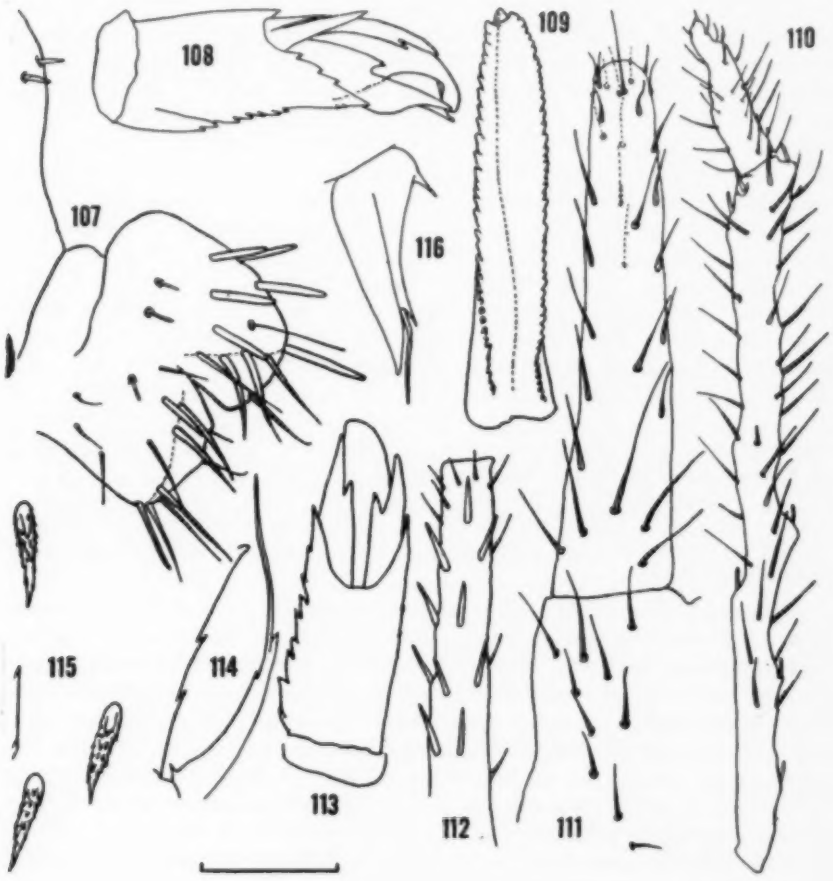
Jataban, Gambia (West Kiang), 6. ix. 57. Under logs in savanna.

DICYRTOMINA ORYZAE sp. n.

(Figs. 107 to 116 and 124)

Female : Size 1·3 mm. (Max. 1·5). Coloration pale green with strong pattern of superficial pigment as in Fig. 124. Body strongly arched posteriorly. Head and thoracic region clothed very sparsely with short, slender setae, without spines. Posterodorsal region with the usual corrugated area bearing cylindrical, truncated spines up to 27 μ long. Anterior bothriotrichium situated on a high papilla, corrugated posteriorly and with supplementary seta

laterally. Two other pairs follow this closely, without well defined papillae. Laterally on the furcal segment, at base of manubrium are 3+3 toothed spines (Fig. 115) arranged as in *Sminthurus stylifer*, q. v. Genital segment (Fig. 107) separated from furcal segment by a distinct suture, just posterior to which there is, on each side, a deep, elongate cleft in which lies the genital bothriotrichium. Anal segment strongly separated with basic plan of chaetotaxy typical for the genus. There are dorsally 10 blunt, cigar-shaped spines—a semicircle of 7,



Figs. 107 to 116.—*Dicyrtomina oryzae*.

Fig. 107.—Anogenital segs. (Holotype), × 1; 108, Claw III, oblique, dorsal view, × 4; 109, Mucro (Holotype), × 2·4; 110, Ant. III and IV (Holotype), × 1; 111, Furca (Holotype), × 1; 112, Tibiotarsus III, inside view, × 1; 113, Claw II, dorsal view, × 4; 114, Empodial appendage of leg I and inner edge of claw (Holotype), × 4; 115, Lateral manubrial setae (Holotype), × 6; 116, Empodial appendage of leg III (Holotype), × 4. (All magnifications quoted are relative to the 100μ scale included in the illustration.)

followed by 2 and then a single one in the position of the median unpaired seta of the perianal chaetotaxy. Among the spines are the usual 1+1 bothriotrichium like hairs. Laterally are 3+3 simple, thin-walled sensillae as in *D. minuta*. The inner median seta (i.e. lying close to the aperture) curved and slender, without a papilla. On the lower anal valves the subanal appendage is simple, spine-like and 53 μ long. Laterally are 1+1 cigar-shaped spines.

Antennae 2·2 head diagonal, with segs. I to IV, 87, 418, 475 and 114 μ resp. No trace of annulation distally on Ant. III which bears 5 sensillae on " knots " at the apex and 5 on the basal part of shaft (Fig. 110). S. O. Ant. III with two rods in separate depressions. Ant. II, bears 3 sensory setae on the shaft, Ant. I with a few short hairs only. Ocelli 8+8, subequal. Leg I with tibiotarsus, claw and EA, 380, 61 and 53 μ resp. Leg II, 399, 65 and 38 μ, resp., and Leg III, 471, 68 and 42 μ resp. Tibiotarsi bear tapering, bluntly pointed, smooth spines on the inner side, which even on leg III (Fig. 112) do not appear to be arranged in well defined rows. Claws typical of the genus, with broad, toothed basal pseudonychia subtended by an outer tunica half-length of claw, and an inner, hood-like tunica extending the full length of the claw (Figs. 108 and 113). Between these lie one or two further pairs of long lamella-like pseudonychia. The claw itself has two inner teeth on all legs (Fig. 114). EA with inner basal tooth and a subapical needle (Fig. 114 and 116). Furca with chaetotaxy as in Fig. 111, all setae smooth. Dens 380 μ more than three times mucro. The dorsodistal seta is 76 μ long or 3/5 mucro. Mucro 122 μ, with both dorsal lamellae strongly toothed. The outer lamella is much more finely toothed than the inner. Tenaculum with 3+3 teeth on rami, basal appendages and high corpus with one apical and one subapical pair of setae. Ventral tube with 1+1 setae on stem, near to apex, and 1+1 on valves. 2+2 strong papillae within the valves and vesicles long and tuberculate.

Male : Unknown as no males were included in the type series or any other material available.

Affinities : The genus includes a large number of inadequately known species but, since the colour pattern is accepted as rather stable, this gives a good indication of whether the form has been encountered previously. Since no described form has the highly distinctive pattern described above, it seems legitimate to regard this as a new species. Among the very few species of which the critical features of chaetotaxy are adequately known, the species is unique in having the median unpaired seta of the perianal chaetotaxy represented by a blunt spine and in having the genital segment separated by a suture from the furcal segment. It belongs to the *D. rufescens* complex on account of the absence of spines from head and thorax and the smooth dental setae. The 3+3 lateral spines at base of manubrium appear to be a valuable taxonomic feature, these being represented in *D. minuta* by straight, simple setae.

Types : Holotype in alcohol and a series of paratypes, some in alcohol and some dissected and mounted, have been deposited in the British Museum (Nat. Hist.).

Type locality : Keneba, Gambia, 10. vii. 56. Swept from rice fields 2 Km. west of Keneba.

COMMENTS ON THE DISTRIBUTION OF SOME FORMS

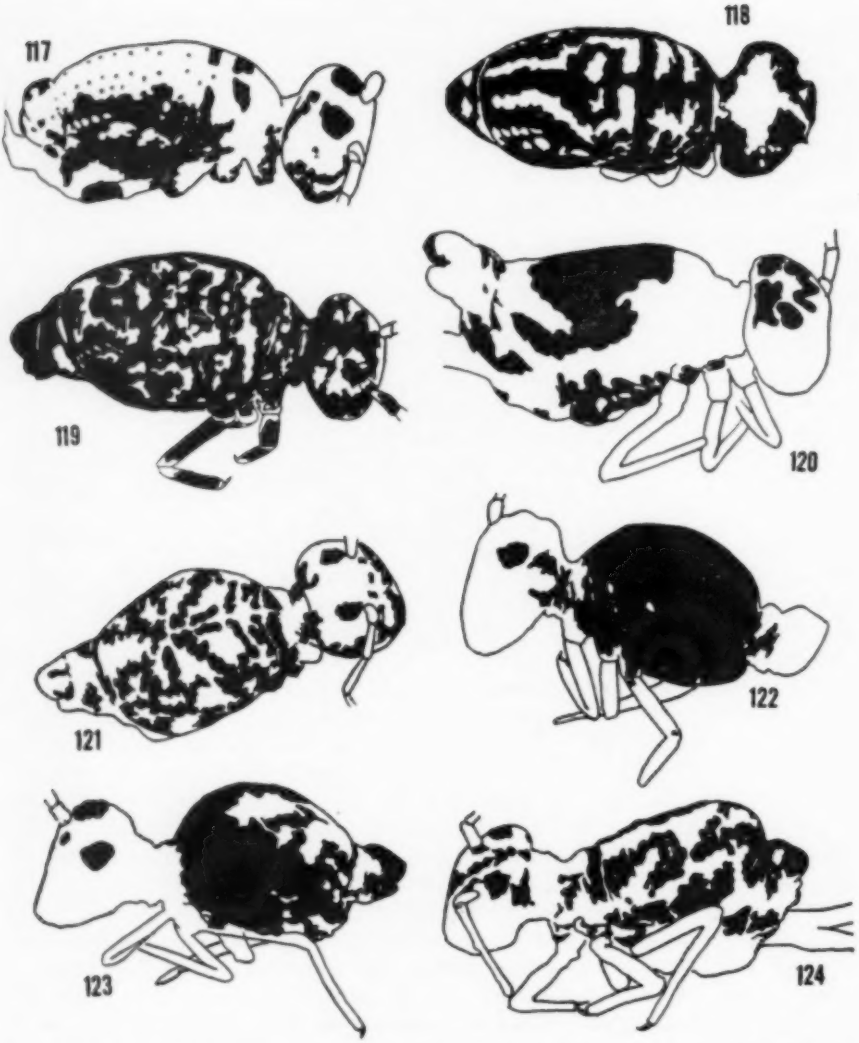
The preceding pages record all the species of Symphypleona that were included in the collection, with the exception of a number of forms represented only by immature material or by single individuals. There were certainly several other species both of *Sminthurides* and *Bourletiella* (lat.) involved.

With regard to those species which are described for the first time in this paper, nothing can be said about their distribution outside the Gambia, but the other forms mentioned do raise points of biogeographical interest.

Very little is at present known about the collembolan fauna of the vast savanna tract which lies south of the Sahara, most expeditions to Africa having tended to concentrate on the more obviously productive tropical forest regions. Wahlgren (1908) appears to have collected little from this type of terrain and reported none of the forms mentioned here. Delamare (1947) recorded three species from Senegal of which one, *Bovicornia coronata* has so far been taken in the Gambia, and it is to be expected that the other two, *Prorastriopes pulchra* and *P. risbeci* will also be found. The same author visited an area of savanna in the Ivory Coast (1950) but recorded no Symphypleona. Of the species here recorded from the Gambia it is striking that two, *Sminthurinus stenognathus* and *Bourletiella spathacea* should previously be known only from the island of Pemba on the east coast. This island is adjacent to that part of the coast where the other end of the northern savanna belt emerges and it therefore seems possible that these two species at least will extend throughout the vegetation zone.

One other point of interest emerges, namely, that two species, *Sminthurides* cf. *ramosus* and *Sminthurus macroceros* show a widely disjunct distribution involving both sides of the Atlantic. The situation is at present, *S. ramosus* is officially recorded only from Hawaii in addition to the present record from the Gambia. However, on page 571 it is shown that the distinctions from *S. sexpinnatus* from Costa Rica may not in fact be specific and on this interpretation the distribution of the species, although still involving enormous distances over water, becomes more logical. The presence of this, at most very closely related group of species in such widely separated areas as West Africa, Costa Rica and Hawaii is at first sight difficult to explain. However, in both the Atlantic and Pacific oceans there are strong, persistent west-blowing wind currents which link all three areas concerned and the question arises, whether these forms show stages sufficiently resistant to allow them to be dispersed over such vast distances.

In the Gambia, *S. cf. ramosus* is characteristic of temporary waters in the savanna which dry out completely and are baked hard for at least four months in the year. Some very resistant stage must therefore exist which might be dispersed on dried soil particles either by birds or by chance inclusion in the aerial plankton. Certainly the conditions to which it would be exposed during such transport could hardly be more severe than those of the normal dry season. It is worthwhile recalling that at this time of year, strong off-shore winds (the " Harmattan ") are a characteristic feature in the Gambia and that minor duststorms are not uncommon. While human transport, especially



Figs. 117 to 124.—Distribution of superficial pigmentation in some of the species described. Not to scale.

Fig. 117.—*Sminthurides gambiae* sp. n.; 118, *Sminthurides avicenniae* sp. n.; 119, *Sminthurinus stenognathus* Börner; 120, *Bourletiella savanna* sp. n.; 121, *Bourletiella alatipes* sp. n.; 122, *Bourletiella gisiniana* sp. n.; 123, *Sminthurus stylifer* sp. n.; 124, *Dicyrtomina oryzae* sp. n.

across the Atlantic cannot be ruled out, it nevertheless seems that long-distance wind transport is a possibility to be seriously borne in mind when considering the biogeography of savanna forms. As shown by G. G. Simpson (1952) the very low probabilities of successful colonisation over a wide barrier such as

the Atlantic, often regarded as " effectively " nil, have on the contrary quite a high probability when the long periods of time available for such transport are taken into account.

The situation in the subgenus *Denisiella* to which *S. ramosus* belongs, suggests that since West Africa is at the up-wind end of the distribution of *S. ramosus* it is on the African Continent that the subgenus arose. On this continent, *S. ramosus* occupies the north savanna part of its range, while in the southern Kalahari area, the corresponding niche is occupied by a closely related but definitely distinct species, *S. serroseta* CB. Distribution by wind currents of *S. ramosus* having brought the group into the Pacific region, the occurrence of the other known species, *S. seurati* in the Tuamotu Islands could be explained as an earlier transportation (possibly from the middle Americas) than that which brought *S. ramosus* to Hawaii.

The occurrence of *Sminthurus macroceros*, also a savanna form, in both the Gambia and in Costa Rica could be explained along the same lines and indeed, other links may be expected to appear when the middle American savanna zone, at present almost unworked, becomes better known. It might be pointed out that *Sminthurides macgregori*, occupying similar habitats to *S. ramosus* might reasonably be expected to occur in the American region, since as mentioned on page 564 the species seems to be parthenogenetic, a fact which, if true, would give it a mathematically far better chance of successfully making a long-distance dispersal of this type.

ACKNOWLEDGMENTS

I am deeply grateful to Professor J. B. Cragg for his interest, advice and help in the preparation of this paper. Dr T. Clay gave valuable advice and I am indebted to the authorities of the British Museum (Nat. Hist.) for facilities of study.

The material was collected in my off-periods whilst employed by the Medical Research Council and I am grateful to my employers for the opportunity to visit the Gambia. In particular, I wish to thank Dr I. A. McGregor, Director of the Medical Research Council Laboratories, Fajara, near Bathurst, Gambia, for his benevolent interest in my general collecting activities.

Special note : The author is at present working on a world revision of the genus *Sminthurides* sensu lat. and would welcome any material of this genus, particularly from tropical regions.

APPENDIX

In connection with the species of *Sminthurides* described in this paper, reference has been made to material in the collection of the British Museum (Nat. Hist.) of *S. spegazzinii* Börner and *S. melanotus* Börner. Material also exists in this collection of a number of European species of which the pregenital setae have been examined, and of *S. appendiculatus* Imms from India in which the original description is lacking in some particulars.

1. *SMINTHURIDES MELANOTUS* Börner 1907

A single, somewhat deteriorated individual in the British Museum collection appears to constitute the only member of Börner's original material of which the whereabouts is at present known. This being so, specimen No. 176 in the B.M. collection, labelled *Sminthurides spegazzinii melanota* Börner, on water plants, La Plata, S. America, Spegazzini coll., is here designated lectotype of the species *Sminthurides melanotus* Börner.

The opportunity is taken to give illustrations of claw I (Fig. 126), claw III (Fig. 127), posterodorsal setae (Fig. 125) and pregenital setae (Fig. 132) of this individual. Unfortunately owing to its condition the chaetotaxy of dens, furca and antennae cannot be illustrated at present. The important points of difference from the most closely related species at present known, *S. gambiae*, have been dealt with in the discussion of that species, namely, the single inner tooth on claw I, short posterodorsal chaetotaxy and a slightly different arrangement of the apical lateral denticulation of claw III.

2. *SMINTHURIDES SPEGAZZINII* Börner 1907

Two specimens in the British Museum collection appear to be the sole surviving representatives of the original material. Under the circumstances, the best specimen (No. 175 of the B.M. collection labelled *Sminthurides spegazzinii* Börner, on water plants, La Plata, S. America, Spegazzini coll.) is here designated lectotype and the other (No. 174) as paratype.

The opportunity is taken to give figures of claw I (Fig. 130), claw III (Figs. 128 to 129) and pregenital setae (Fig. 131) of the lectotype. It will be noted that in claw III there is one basal and one subapical pair of lateral teeth only.

3. *SMINTHURIDES APPENDICULATUS* Imms 1912

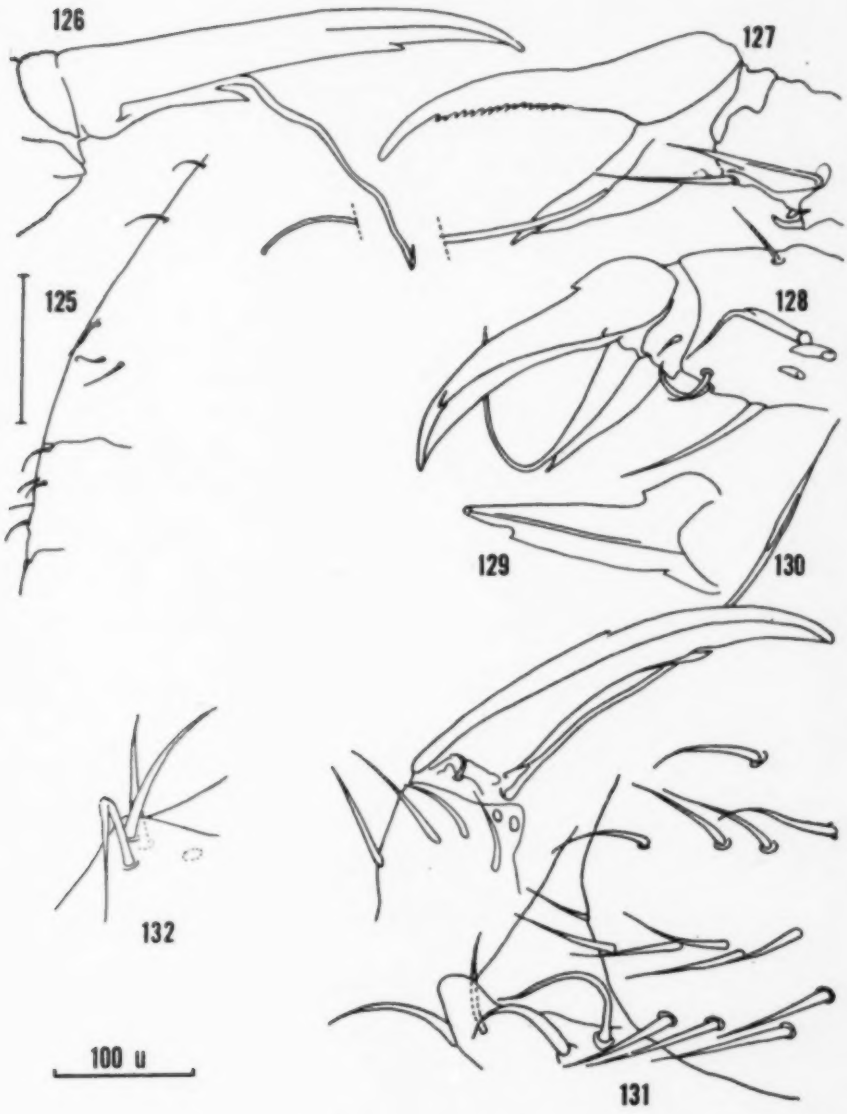
A single paratype of this species exists in the British Museum Collection, mounted and in a deteriorated condition. This differs strongly from the allied *S. penicillifer* in that Claw III has numerous lateral serrations as in *S. melanotus*. Claw I (contrary to description) has a single, distinct inner tooth and, as in all other members of the group, EA I is unilaterally lamellate at the apex. It has not been possible to examine the guarding seta or the pregenital setae.

4. Material from various sources has been examined of the following species, enabling them to be classified according to the number of pregenital setae. The Gambian species are included.

1+1 pregenital setae. *S. aquaticus*, *S. a. viridulus*, *S. schötti*, *S. signatus*, *S. distinctus* and *S. parvulus*.

2+2 pregenital setae. Small, simple and unmodified. *S. malmgreni*, *S. macgregori* and *S. sphaeridioides*.

2+2 pregenital setae enlarged and thickened. *S. penicillifer*, *S. melanotus*, *S. spegazzinii*, *S. gambiae* and *S. avicenniae*.



Figs. 125 to 132.—*Sminthurides melanotus* and *S. spegazzinii*.

Fig. 125.—*S. melanotus* Profile of posterodorsal region and scale indicating size of mucro ; 126, *S. melanotus* Claw I, × 4 ; 127, *S. melanotus* Claw III, × 4 ; 128, *S. spegazzinnii* Claw III, lateral view, × 3 ; 129, *S. spegazzinii* Claw III, dorsal view, × 3 ; 130, *S. spagazzinii* Claw I, lateral view, × 3 ; 131, *S. spagazzinii* Lower anal valve and pregenital setae (Lectotype), × 4 ; 132, *S. melanotus*. Pregenital setae (Lectotype), × 4.
(All magnifications quoted are relative to the scale included in the illustration.)

REFERENCES

BERTRAM, D. S., MCGREGOR, I. A. & MCFAZDEAN, J. A. (1958). Mosquitos of the Colony and Protectorate of the Gambia. *Trans. R. Soc. trop. Med. Hyg.* **52** : 135.

BÖRNER, C. (1907). Collembolen aus Ostafrika, Madagaskar und Südamerika. Voeltzkow, *Reise in Ostafrika* 1903–1905 **2** : 147–178.

BÖRNER, C. (1912). Collembolen aus Zentralafrika. *Wiss. Ergebn. deutsch. Zentr.-Afr.-Exped.* **4** : 283–284.

DELAMARE-DEBOUTEVILLE, C. (1951 c). *Microfaune du Sol des Pays Tempérés et Tropicaux.* Paris.

DELAMARE-DEBOUTEVILLE, C. (1952). Trois nouvelles espèces de Collemboles de la Cote d'Ivoire. *Rev. franç. Entom.* **19** : 240–243.

DELAMARE-DEBOUTEVILLE, C. (1953). Collemboles du Kilimandjaro récoltés par le Dr George Salt. *Ann. Mag. nat. Hist.* (12) **6** : 817–830.

DENIS, J. R. (1931). Collemboles de Costa Rica avec une contribution au species de l'ordre. (Contributo alla conoscenza del " Microgenton " di Costa Rica II.) *Boll. Lab. Zool. gen. agr. Portici* **25** : 69–171.

DENIS, J. R. (1933). Collemboles de Costa Rica II. (Contributo alla conoscenza della " Microgenton " di Costa Rica III.) *Boll. Lab. Zool. gen. agr. Portici* **27** : 222–322.

FOLSOM, J. W. (1932). Hawaiian Collembola. *Proc. hawaii. entom. Soc.* **8** : 51–80.

GAMBLE, D. P. (1949). *Contributions to a socio-economic survey of the Gambia.* London. H.M.S.O.

GISIN, H. (1946). Revision des espèces suisses du genre *Bouletiella* lat. (Collembola.) *Mitt. schweiz. entom. Ges.* **20** : 249–261.

IMMS, A. D. (1912). On some Collembola from India, Burma, and Ceylon with a catalogue of the Oriental species of the order. *Proc. zool. Soc. Lond.* **1912** : 80–125.

MARLIER, G. J. (1944). Collemboles. *Explor. Parc Nat. Albert, Miss. H. Damas* (1935–36). *Fasc.* **13** : 1–11.

MAYNARD, E. A. (1951). *A monograph of the* Collembola *or springtail insects of New York State.* Ithaca, N.Y.

MCGREGOR, I. A. & SMITH, D. S. (1952). A health, nutrition and parasitological survey in a rural village (Keneba) in West Kiang, Gambia. *Trans. R. Soc. trop. Med. Hyg.* **46** : 403.

MURPHY, D. H. (1960). Some records and redescriptions of British Collembola, Part II.—Symphypleona, with a description of *Bourletiella cragyi* sp.n. Proc. R. ent. Soc. Lond. (B) **29** : 57–64.

SCHÖTT, H. (1893). Beiträge zur Kenntnis der Insektenfauna von Kamarun. I. *Collembola. Bih. Svenska Vetensk.-Akad. Handl.* (Zool.). **19** (Afd. 4) No. 2 : 1–28.

SCHÖTT, H. (1927). Kamarunische Collembolen. *Jber. Gymn. Linköping.* 1–40.

SIMPSON, G. G. (1952). Probabilities of dispersal in geologic time. *Bull. Amer. Mus. nat. Hist.* **99** : 163–176.

STACH, J. (1956). The apterygotan fauna of Poland in relation to the world fauna of this group of insects. VI. Sminthuridae. *Acta mongr. Mus. Hist. nat. polska Akad.* (6) : 1–27.

STACH, J. (1957). The apterygotan fauna of Poland in relation to the world fauna of this group of insects. VII. Neelidae and Dicyrtomidae. *Acta monogr. Mus. Hist. nat. polska Akad.* (7) : 1–113.

WAHLGREN, E. (1906). Apterygoten aus Ägypten und aus dem Sudan nebst Bemerkungen zur Verbreitung und Systematik der Collembolen. *Res. swed. zool. Exped. Egypt* No. 15 : 1–72.

WAHLGREN, E. (1908). I. Collembola. *Wiss. Ergebn. schwed. zool. Exped. Kilimandjaro* (19) : 1–10.

THE DURATION OF PREGNANCY IN RHESUS MONKEYS *MACACA MULATTA*

BY

P. L. KROHN*

Department of Anatomy, The Medical School, University of Birmingham

[Accepted 10th November 1959)

The gestation period has been estimated in 34 pregnancies which have occurred in the Birmingham colony of rhesus monkeys. The placental sign could be identified in 16 of them and the gestation periods in this group varied between the limits of 158 and 173 days. No placental sign could be recognized in the other 18 pregnancies and the records of menstrual bleeding could not be interpreted to give reasonably consistent estimates of the duration of pregnancy.

One prolonged labour is described in detail and the exceptionally heavy baby, weighing 840 g, was finally born after a normal gestation period of 165 days.

CONTENTS

	Page
Introduction	595
Description of pregnancy	595
Discussion	596
Gestation period	596
References	599

INTRODUCTION

The course of parturition in monkeys has been described and photographed on several occasions (Hartman, 1928 ; Spiegel, 1930 ; Philipp, 1931). The following description of a birth in the Birmingham colony of monkeys is given because of its unusual features, and because it drew attention to the difficulty of determining the probable date of parturition when only the records of menstrual bleeding are available and the date of insemination is unknown.

DESCRIPTION OF PREGNANCY

OM 731 (*Macaca mulatta*) arrived in the colony in October, 1954. Her sexual skin showed the swellings characteristic of late adolescence ; her permanent dentition was not yet fully erupted and she weighed 5200 g.

Subsequently, she delivered two normal babies in September, 1955 (female, birth weight 470 g.) and April, 1956 (male, birth weight 510 g.). Her supply of milk was inadequate on both occasions and the babies had to be brought up by hand.

Her third and exceptional pregnancy was confirmed clinically in July, 1957. The first signs that labour was imminent occurred on the 28th September, 1957, when the monkey began to pick at her vulva. Labour did not progress any further during this or the next two days, but the monkey remained uneasy and continued to pick at her vulva.

At about 10.30 p.m. on the 30th September the monkey became more restless and by 11.30 p.m. uterine muscular contractions were obviously taking

* Nuffield Senior Gerontological Research Fellow.

place about every five minutes. The muscles in the small of the back and the anterior abdominal wall were also contracting in attempts to expel the foetus. Strong contractions continued—although the animal remained quiet and did not cry out in the manner described by others—but it was not until 1.20 a.m. that the vulva began to widen. By 2 a.m. the vulva had widened further ; contractions were occurring every two or three minutes and increasing in intensity. At 2.20 a.m. the head was just beginning to descend with the strengthening contractions and at 2.35 a.m. it was visible in the vagina during contractions. Further strong efforts were made by the monkey to expel the foetus but without much success. By 3.25 a.m. about half the head was free. Birth took place at 3.40 a.m., the head and the rest of the body being expelled in one strong contraction. The mother immediately picked up the baby and began to lick it.

For the next hour the mother lay, completely exhausted, on the floor of the cage and made no effort to move. The baby was closely grasped to her chest with the umbilical cord stretched tightly across the body to the vulva. As there was no sign that the placenta would be expelled from the vagina the cord was tied off and the placenta removed manually by traction on the cord. Several blood clots were expelled ten to fifteen minutes later.

The mother was very exhausted for the next day or two and the flow of milk was slow to develop and insufficient. The baby (a male which weighed 840 g.) was given supplementary feeds, and though he gradually lost 135 g. in the next fifteen days he was always strong and lively, and regained his birth weight after six weeks.

The monkey became pregnant again in 1958 and delivered a normal male (birth weight 610 g.).

DISCUSSION

This labour differs in two respects from the usual descriptions. First, it was greatly prolonged both in the early stages and in the expulsive stage. According to Hartman's (1928) report the placenta had been expelled within 75 minutes of the onset of labour, and twenty minutes later had been eaten. Similarly, Phillipp (1931) believed that young multiparae might complete the process in as little as twenty minutes though he mentioned a 32-hour long labour leading eventually to a dead birth, which was observed in Hartman's colony. Second, it resulted in the birth of a baby which weighed considerably more than any other rhesus macaque baby so far noted (Hartman, 1932, up to 660 g. ; Van Wagenen, 1950, 300 to 670 g. ; Schultz, 1933, 400 to 500 g.; our own records apart from this pregnancy, 390 to 540 g.). The size of the baby probably accounts for the length and difficulty of the labour.

All observers remark on the repeated inspections of the vulva with their fingers during labour. It was very noticeable, however, that the mother confined her inspections to the surface and made no deeper examination which might have contaminated the birth canal.

GESTATION PERIOD

It was only when trying to work out the likely date of conception in this

TABLE 1

Details of pregnancies in which the "placental sign" evidently occurred.

Monkey No.	Pregnancy	Period of "placental sign" bleeding	Estimated (days) gestation period
OM 453	First	6.9.42–27.9.42	165
OM 453	Second	15.2.44–17.3.44	170
OM 453	Third	21.3.47–3.4.47	168
OM 454	Fourth	28.7.47–31.7.47 5.8.47–8.8.47	172
OM 485	First	12.2.41–14.2.41 and 25.2.41–28.2.41	165
OM 495	Second	6,7 & 13.10.44	159
OM 495	Third	27.2.46–12.3.46	169
OM 507	First	18.3.42–28.3.42	158
OM 635	Third	21.1.54–27.1.54 30.1.54–2.2.54 and 7.2.54–8.2.54	163
OM 635	Fourth	21.12.54–2.1.55	164
OM 635	Sixth	2.10.57–5.10.57 and 9, 13 & 19–22.10.57	158
OM 635	Seventh	15.2.59–19.2.59 23.2.59–24.2.59 and 1 & 2.3.59	163
OM 653	First	10.12.51–13.12.51 24.12.51–28.12.51 1.1.52 and 5–7.1.52	175
OM 697	First	7.2.56–9.2.56 19.2.56–22.2.56 and 7.3.56–9.3.56	169
OM 697	Second	3.12.58–6.12.58 and 14.12.58–21.12.58	167
OM 731	Third	7.5.57–11.5.57 and 26.5.57–28 5.57	165

particular pregnancy that it was realized how variable the circumstances surrounding the beginning of a pregnancy in the monkey may be. The main source of confusion seems to be in deciding how to infer the date of conception from the periods of menstrual bleeding which may have been observed, and how to distinguish a normal bleeding from a bleeding which relates to the implantation of the embryo and the formation of the placenta.

Hartman in his large monograph (1932) discusses "the placental sign" in considerable detail. He believes that it is always present and that it begins 15 to 22 days after fertile coitus and lasts for 13 to 32 days (average 23·3 days). Very variable in intensity from day to day, the bleeding may only tinge the lavage.

An analysis of our own records of thirty-four births divides pregnancies into three groups. First, those in which a placental sign (by Hartman's definition) can be said to have occurred (see Table 1). The gestation period

TABLE 2

Details of pregnancies in which no "placental sign" was observed.

Monkey No.	Pregnancy	Last mentrual period	Gestation period (days)
OM 401	First	14.2.46–18.2.46	129
OM 453	Fourth	14.7.48–19.7.48	137
OM 495	First	1.7.42.–7.7.42	139
OM 606	First	10.10.51–14.10.51	163
OM 625	First	29.1.51–1.2.51	108
OM 625	Second	13.9.54–15.9.54	177
OM 635	Second	3.12.53–6.12.53	172
OM 635	Fifth	15.5.56–22.5.56	129
OM 653	Second	23.2.53	144
OM 666	First	28.12.53–29.12.53	147
OM 731	First	16.5.55–18.5.55	104
OM 731	Second	12.11.55–15.11.55	156
OM 731	Fourth	21.4.58–28.4.58	141
OM 584	First	29.6.58	172

is calculated on the basis that conception occurred 17 days before the start of the placental sign. Second, those in which the last menstrual period seemed

to have all the characteristics of a normal period and in which there seems to be no reason for recognizing a placental sign (see Table 2). Conception is presumed to have occurred on the eleventh day of the cycle which began with the last bleeding. In the third group of four pregnancies the records were too confusing to permit any reasonable assessment of the date of conception. One animal (OM 454) provides three of these confusing pregnancies, including the very long pregnancy already reported by Eckstein (1944).

It is fairly clear that the estimates of the duration of pregnancy (158–175 days) agree very well with Hartman's range of 149–180 days, and Van Wagenen's (1945) average of 168 days, in the sixteen cases when it could confidently be asserted that a placental sign had taken place. On the other hand, there are almost as many (14) instances where it is impossible to say from the records whether the last bleeding is a true menstrual bleeding or a placental sign. The wide scatter of gestation periods in this second group is particularly noteworthy. Some of the intervals are such that the gestation period would be about the same as in Group I if the last bleeding, though apparently normal, was really a placental sign, an assumption which would involve adding about 30 days to the calculated figures. The others would remain either much shorter or become much longer than 165 days. It can only be supposed, therefore, that pregnant monkeys whose gestation periods seem to be short, may undergo one or more periods of overt bleeding which are indistinguishable from a normal menstrual period or that the placental sign may have been microscopic and have passed unrecognized in some of these cases. Certainly in one pregnancy (OM 731 (2)) the monkey immediately became pregnant when mated soon after the first post-lactational bleeding, and gave birth to her baby 155 days after the presumed day of conception without any further obvious menstrual bleeding of any sort. In any event, the extremely long pregnancy described by Eckstein (1944) and the other anomalous (usually short) pregnancies shown in the Tables cannot, as yet, be fitted into any standard pattern.

REFERENCES

Eckstein, P. (1944). Unusually long pregnancy in a macaque. *J. Anat., Lond.* **78** : 147.

Hartman, C. G. (1928). Description of parturition in monkey, pithecus (Macacus) rhesus, together with a data on gestation period and other phenomena incident to pregnancy and labor. *Johns Hopk. Hosp. Bull.* **43** : 33.

Hartman, C. G. (1932). Studies in the reproduction of the monkey (Macacus (Pithecus) rhesus) with special reference to menstruation and pregnancy. *Contr. Embryol. Carneg. Instn.* **23** : 1.

Philipp, E. (1931). Physiologie und Pathologie der Geburt be Affen. *Zbl. ges. Gynäk.* **55** : 1776.

Schultz, A. H. (1933). In *The anatomy of the rhesus monkey*. Ed. C. G. Hartman & W. L. Straus, Jr. London.

Spiegel, A. (1930). Beobachtungen über den Sexualzyklus, die Gravidität und die Geburt bei Javamakaken (*Macaca irus mordax* Thomas & Wroughton *cynomolgus* L.). *Arch. Gynaek.* **142** : 561.

Van Wagenen, G. (1945). Optimal mating time for pregnancy in monkey. *Endocrinology* **37** : 307.

Van Wagenen, G. (1950). In *The care and breeding of laboratory animals*. Ed. E. J. Farris, New York.

THE EVOLUTION OF THE PULMONATE GENITAL SYSTEM

BY

C. J. DUNCAN

Department of Zoology, University of Liverpool

[Accepted 10th November, 1959]

(With 1 figure in the text)

The evolution of the pulmonate genital system is traced from a prototype exemplified by the tectibranch *Acteon*. Many features remain almost unchanged in the genera studied, but there is a progressive degree of separation and specialization of the male and female ducts. Some genera of the Ellobiidae, such as *Pythia*, are undoubtedly primitive. However, it is suggested, following an investigation of the reproductive system of *Chilina robustior*, that the Chilinidae may stand closest to the ancestors of the Stylommatophora and the Hygrophila.

The sexual cycle in *Physa* is compared with the protandric sequence found in the primitive Ellobiidae. Similarly, the course of the vas deferens through the mantle wall and the development of the penis from a separate anlagen are also thought to be relics of the ancestral condition.

CONTENTS

	Page
Introduction	601
Tectibranchia—*Acteon*	603
The Ellobiidae	604
The Chilinidae	604
The Stylommatophora	605
The Hygrophila	606
Discussion	607
Acknowledgments	609
References	609

INTRODUCTION

Following previous publications on the functional anatomy of pulmonate reproductive organs, the present account attempts to suggest possible evolutionary lines and homologies of the genital systems within the sub-class. Relationships are clarified by the use of a common staining technique, Heidenhain's azan giving a characteristic histological picture at each stage of maturation in the various organs. The same picture is given by the organ in the different genera. In addition to the representatives already described (Duncan 1958, 60a), *Chilina robustior* and *Helix aspersa* were also investigated. Information on other groups was obtained from the publications of Fretter & Graham (1954) and Morton (1955b) and also from the reviews by Hubendick (1947) and Morton (1955a). However, this survey of pulmonate reproductive systems is far from complete and only a small selection of species has been examined.

The Gastropoda is divided into three sub-classes, Prosobranchia, Opisthobranchia and Pulmonata. The two latter groups have both probably evolved from a prosobranch stock, the more advanced opisthobranchs specialising in the loss of the shell. *Acteon* is a primitive, shelled opisthobranch and has

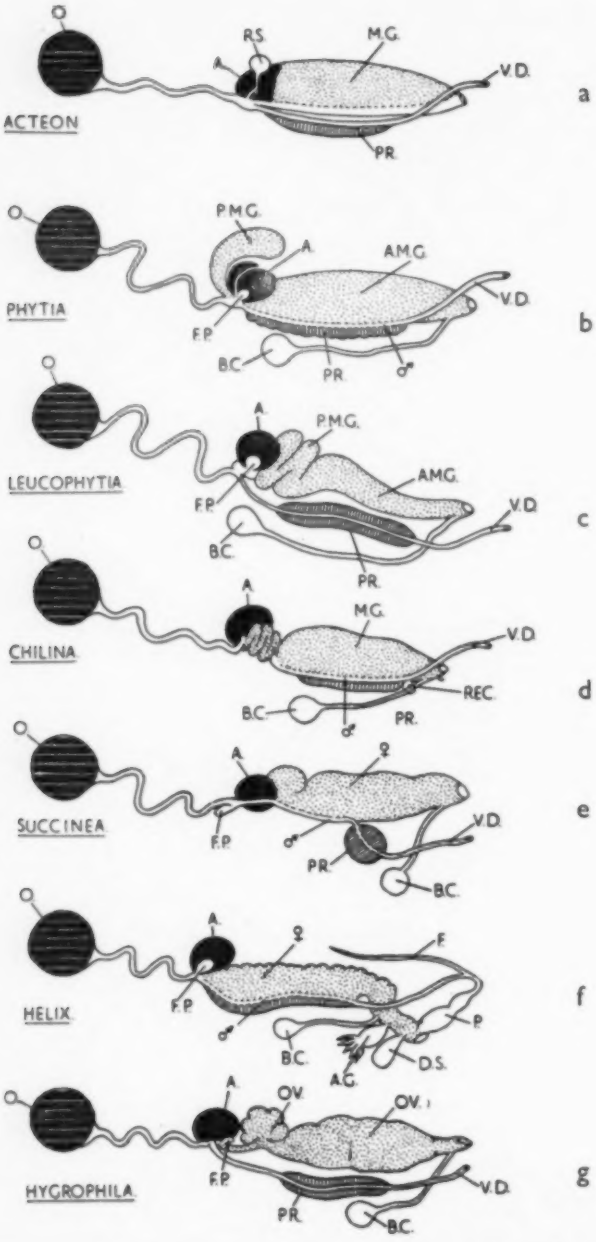


Fig. 1.—Diagrams of the reproductive organs of *Acteon* and selected pulmonates.

(*Explanation foot of facing page*)

much in common with both the Prosobranchia and with the primitive pulmonates (Morton, 1958). The present account uses the description of *Acteon tornatilis* by Fretter & Graham (1954) as its starting-point and as the prototype for the evolution of the pulmonate reproductive systems.

Acteon was originally classified within the Tectibranchia, but Morton (1958) has basically followed Odhner in dividing the Opisthobranchia into eight orders, *Acteon* being included in the primitive Cephalaspidea. The Pulmonata is divided into two orders, the Basommatophora and the Stylommatophora. The former includes primitive families, the Ellobiidae and the Chilinidae (Actophila) and the more advanced freshwater families, the Hygrophila. The Stylommatophora are essentially terrestrial, with the familiar snails and slugs, although the amphibious Succineidae are less specialized in habitat and structure.

TECTIBRANCHIA—*ACTEON*

Various suggestions have been made as to which group of the gastropods may have given rise to the pulmonates. Morton (1955a) has discussed the evidence for the relationships of primitive pulmonates to prosobranchs and to tectibranchs. He points out that although there is close tie between the basal members of these three groups, the existing tectibranchs are, of course, too specialized to be the ancestors of primitive pulmonates. However, there is general agreement that the Ellobiidae is the most primitive family included in the Pulmonata and amongst the tectibranchs the genital system of *Acteon tornatilis* has the same basic arrangement as that found in the ellobiids, (see Fig. 1a). *Acteon* is a hermaphrodite and the male and female ducts are separate from their origin at the anterior end of the hermaphrodite duct, (Fretter & Graham, 1954). The male duct has prostatic gland cells projecting from its wall, although anteriorly the prostate narrows and the vas deferens becomes a ciliated, non-glandular channel which joins the penis. As Morton points out, this development of an enclosed, anterior vas deferens in *Acteon* resembles the condition existing in the Ellobiidae. The female system of *Acteon* includes albumen and mucous glands and the duct of the receptaculum seminis is long. Following Fretter (1946) the term receptaculum seminis is used in the present investigation for the sac at the upper end of the genital duct and in the pulmonates this is replaced by the fertilisation sac or pocket, which lacks the long duct of the receptaculum. The term bursa copulatrix has been retained for the receptacle used for the storage of foreign sperm, the duct of

---

(a) *Acteon tornatilis*, based on the description of Fretter and Graham (1954).
(b) *Phytia myosotis* modified after Morton (1955b).
(c) *Leucophytia bidentata* from Morton (1955a).
(d) *Chilina robustior*.
(e) *Succinea pfeifferi*.
(f) *Helix pomatia* after Fretter (1946).
(g) Generalized member of the Hygrophila, based primarily on *Physa fontinalis*.

A.—albumen gland ; A.G.—accessory mucus gland ; A.M.G.—anterior mucus gland ; B.C.—bursa copulatrix ; D.S.—dart sac ; F.—flagellum ; F.P.—fertilization pocket ; M.G.—mucus gland; O.—ovotestis ; OV.—oviduct ; P.M.G.—posterior mucus gland ; PR.—prostate ; REC.—receptacle for sperm ; R.S.—receptaculum seminis ; V.D.—vas deferens.

which opens into the vagina at the base of the oviduct (see Fig. 1). Although no bursa copulatrix is present in *Acteon*, the fundamental pattern of the genital system which is found throughout the pulmonates is clearly evident.

THE ELLOBIIDAE

Amongst the unspecialized members of the Ellobiidae, it is only in *Pythia* that the seminal groove remains open from the common genital aperture to the male opening, resembling the condition found in most tectibranchs (Morton, 1955a).

In *Ovatella* (=*Phytia*) *myosotis*, the hermaphrodite portion of the genital duct is glandular, with an incomplete division into male and female tracts. The female portion of the duct is supplied with anterior and posterior mucus glands and the two albumen glands open into the thin-walled fertilization pouch close to the opening of the little hermaphrodite duct. The sperms pass along the male groove and this is lined by prostatic epithelium. From the female aperture, the vas deferens continues as a separate, closed duct to the penis. The duct of the bursa copulatrix is long and opens into the genital vestibule, (Morton, 1955b). Within the Ellobiidae, various specializations are found in the evolution of the genital system and of these the separation of the prostate to form a closed tube is of special significance. This condition is found in *Leucophytia bidentata*, (see Fig. 1c), where the male and female ducts separate at the base of the little hermaphrodite duct. The schematic plan of the genital system shown in Fig. 1c corresponds closely with the general arrangement found in the four families contained in the Hygrophila, although this is probably an example of parallel evolution only.

THE CHILINIDAE

Whilst the unspecialized members of the Ellobiidae illustrate the most primitive level of evolution in the Pulmonata, Hubendick (1945 and 1947) regards the Chilinidae and Amphibolidae, amongst recent forms, as being the most closely allied to the higher limnic Basommatophora. A brief investigation was therefore made of sections prepared from material of *Chilina robustior* obtained from Chile and this confirmed the primitive nature of the genital system and the arrangement is shown diagrammatically in Fig. 1d. The glandular portion of the genital duct is structurally hermaphrodite, although subdivided into male and female tracts. The female region is supplied with well-developed mucous glands and the male groove is lined by an extensive prostatic epithelium. A short distance before the genital duct opens at the female aperture, the vas deferens separates and continues as a closed duct which joins the simple penis. The relatively long duct of the bursa copulatrix opens into the lower, anterior portion of the female duct, and at the point where the vas deferens leaves the genital duct a small receptacle for the storage of sperm is found, (see Fig. 1d, REC). Spermatozoa were found in both this receptacle and the bursa and the precise function of these two storage organs is unknown, but the receptacle at the separation of the male and female tracts probably serves as an accessory bursa.

After staining with azan, the histology of the different gentital organs of

Chilina closely resembles that found in the higher Basommatophora and in *Succinea*. Of special interest are the component cells of the female tract and the prostatic epithelium. The female system is divided into two portions ; posteriorly it is greatly convoluted and tracts of cuboidal, ciliated cells are found as well as those of the glandular type. Anteriorly, the female part of the genital duct is simple and sac-like and is formed of columnar, glandular cells which stain blue with azan and resemble the characteristic secretory cells which occur in the oviduct of members of the Hygrophila. In spite of the incomplete separation of the male and female tracts, these two regions of the female system of *Chilina*, therefore, show a strong resemblance to oviducts II and III of the Physidae and Lymnaeidae, (Duncan, 1956 and '58).

THE STYLOMMATOPHORA

With the general histological similarity, incomplete separation of the male and female systems and arrangement of the reproductive organs, it would appear that in its structure the genital system of *Chilina* might closely resemble the ancestral conditions of the Stylommatophora. The amphibious Succineidae are among the primitive members of the Stylommatophora and a description of the reproductive system of *Succinea pfeifferi* has been given elsewhere (Duncan, 1960b), whilst the arrangement of the genital organs is shown diagrammatically in Fig. 1e. Although the male groove of *Succinea* is functionally separate, the two tracts remain in communication for about half the length of the genital duct ; the vas deferens then emerges and enters the prostate which, therefore has no connection with the female portion of the genital system. The cells of the prostate are similar to the glandular cells which line the male groove of *Chilina*. Similarly, the ovotestis, little hermaphrodite duct, albumen gland and bursa copulatrix of *Succinea* correspond with the descriptions of the same organs of members of the Ellobiidae and Chilinidae. Other workers on the Succineidae (Quick, 1933 and '36) have described a pair of " seminal vesicles " opening into the hermaphrodite duct close to the point where it enters the albumen gland. From their histology, they appear to be identical with the fertilization pocket found close to the albumen gland in the higher, limnic Basommatophora. They are probably homologous with the fertilization pockets or sacs found throughout the Pulmonata and so this terminology is adopted (Duncan, 1960b).

The reproductive system of a more specialized stylommatophoran, such as *Helix pomatia*, appears to be more complex than that of *Succinea*, but this is largely due to the development of accessory genital organs, the mucus glands, flagellum and dart sac, (see Fig.1f), the last being concerned with the elaborate courtship which precedes pairing in this genus. Otherwise, the basic arrangement and histological structure of the component organs remains the same as in *Succinea*, the genital duct being incompletely separated into male and female systems for the greater part of its length. Although the male tract is lined by the characteristic prostatic cells, a point of difference between the two genera occurs in the absence, in *Helix*, of a definite prostate gland.

Both Hubendick (1945) and Morton (1955a), after a study of the external features and the digestive, excretory, genital and nervous systems of many

of the more primitive pulmonate families, consider that it is only amongst the ellobiids that one finds forms sufficiently primitive to serve as ancestors to the Stylommatophora. Undoubtedly, among its more primitive genera, the family Ellobiidae contains ideally unspecialized members from which, theoretically, many of the higher families could be derived. However, after an examination of *Chilina*, I think that, from a consideration of the reproductive system alone, the Chilinidae may well stand close to the ancestral group of the Stylommatophora. The genital system, although showing an advance over the condition in *Pythia*, is essentially unspecialized, the development of the second sperm receptacle and the posterior portion of the female tract being the only advances from the primitive condition. Hubendick (1947) and Morton (1955a) consider that the family exhibits relatively primitive characters, the nervous and digestive systems being apparently unspecialized, and it is possible, therefore, that the Chilinidae is one of the basal stocks contained within the Pulmonata.

THE HYGROPHILA

The four families of the Hygrophila, the Physidae, Lymnaeidae, Planorbidae and Ancylidae, have many features in common and probably form a natural group of monophyletic origin. Their genital systems exhibit certain differences and the possible evolutionary relationships between them are discussed in a subsequent publication. Fig. 1g shows diagrammatically the reproductive system of a generalized member of the Hygrophila. Of importance is the specialization of complete separation of the male and female ducts throughout the whole of their length. The latter has become differentiated into distinct regions, whilst the former is supplied with a prostate gland. On the other hand, the Hygrophila retain some of the features of the primitive pulmonates. Thus, fertilization pockets associated with the region of the albumen gland are present and the male and female apertures are separate. Among the groups comprising the Basommatophora, the Hygrophila are clearly the most advanced and of the remaining families it is difficult to suggest which might be ancestral to them. Hubendick (1947) states : " the recent forms nearest allied to the ancestors of the higher limnic Basommatophora, belong to the Chilinidae and Amphibolidae." The arrangement of the reproductive system of *Chilina* is on the same level of evolution as the more primitive members of the Ellobiidae. In certain genera (e.g. *Leucophytia*), amongst the ellobiids, the male duct with its prostate has become separate from the anterior mucus gland, although this is probably an example of parallel evolution with the condition existing in the Hygrophila. However, we must agree with Hubendick that the Chilinidae and the Hygrophila have certain features in common, chiefly in the differentiation of the female tract. The anterior and posterior regions of the female system of *Chilina* appear to correspond with oviducts II and III of the Physidae (see Duncan 1958). Hubendick (1947) has shown that two fundamentally different types of prostate are found in the Hygrophila, although both are characterized as organs with a large secretory surface. In the Lymnaeidae, the surface enlargement is achieved by the widening of the vas deferens and, with certain exceptions, by the development of inwardly directed folds in its walls. In the Physidae, Planorbidae and Ancylidae, however, he has shown that the prostatic follicles

are formed by folds and evaginations which develop in an outward direction and are undoubtedly homologous in these three families. The two types of prostate are markedly different in histology and staining reactions ; the main secretory elements of the Lymnaeidae were found to be tall, narrow columnar cells, packed with granules, whilst in the other three families the prostatic cells are large and cuboidal (Duncan, 1960a). It is interesting to note that the histology of the prostate of the ellobiids, described and figured by Morton (1955b), appears to correspond most closely with the prostatic cells found in the Lymnaeidae whilst the prostate of the Physidae, Planorbidae and Ancylidae seems to be homologous and identical in staining reaction with the glandular epithelium lining the male tract of *Chilina*.

To sum up, both the Ellobiidae and Chilinidae lie close to the base of the pulmonate stock and the Stylommatophora and the Hygrophila have probably originated from forms allied to these families. From a study of the morphology and histology of the genital systems, it is suggested that the Chilinidae stand nearer to both these groups than do the Ellobiidae.

DISCUSSION

From a consideration of the reproductive system, therefore, the pulmonates appear to constitute a natural group and in spite of increasing specialization, the same basic pattern of the genital organs can be traced throughout the order. Certain features remain almost unchanged in all the genera studied. For example, the ovotestis, little hermaphrodite duct, bursa copulatrix and albumen gland of *Acteon* persist with only slight alteration of form or basic histology. The secretory product of the albumen gland in many of the higher pulmonates is galactogen, a galactose polymer. Following the first description of this substance by Baldwin and Bell (1938) in *Helix*, it has also been found in *Lymnaea stagnalis* (Holm, 1946) and *Physa fontinalis* (Duncan, 1958). Since the histological structure of the albumen gland seems so constant, it is probable that galactogen is used as the food-store for the developing embryos within the egg capsule in the majority of pulmonates. As outlined above, there is a progressive degree of separation and specialization of the male and female ducts.

The pulmonates differ from the prosobranchs by being universally hermaphroditic, but Morton has described a protandrous sexual cycle in two members of the Ellobiidae, *Carychium tridentatum* (1954) and *Leucophytia bidentata* (1955b). In these species the gonad shows a phase of sperm production which is gradually replaced by a phase of ovogenesis. In *Carychium* the penis and vas deferens were found to be present only in specimens collected in July and August, during the male phase, whilst in *Leucophytia* the glandular section of the male duct disappears during the female phase. Correlated with these changes, the glandular portions of the female duct in both these species gradully increase in size, reaching maximum development during the female phase. During the development of the female organs, the sperms, once liberated from the ovotestis, are stored in the glandular portion of the hermaphrodite duct. Copulation was never observed in either species, but sperm was found in the bursa from late March onwards although no penis was present in *Carychium* at this time.

These results are of special interest when compared with the condensed protandry described in the life cycle of *Physa fontinalis* (Duncan, 1959a). In the development of both *P. fontinalis* and *Lymnaea stagnalis* (Holm, 1946 and Fraser, 1946) the ovotestis initially contains only spermatogonia, but oogonia soon develop in the same acini. The sperm, however, are mature before the ova are fully developed. In correlation with this, the male system develops faster than the female. This is especially noticeable in specimens of *P. fontinalis* collected during the winter months. The vas deferens, prostate and penis are completely developed and fully functional, whilst the oviduct and albumen gland remain small and immature and are frequently difficult to distinguish in a dissection of the animal. The following spring, the female system develops rapidly and quickly reaches maturity. Spat hatching in June and reaching sexual maturity in August, so completing development in six to eight weeks, show a much less marked protandric sequence. The male organs become fully functional only a short time before the female duct and its accessory organs reach maturity, development of the two systems proceeding almost simultaneously. Morton (1955a) suggests that protandrous hermaphroditism is " the general rule among the more primitive sections of both the Pulmonata Basommatophora and the Opisthobranchia Tectibranchia " and it seems most probable that the life cycle described for *P. fontinalis* represents a major evolutionary advance towards the condition of simultaneous hermaphroditism, whilst still exhibiting traces of the ancestral cyclical sequence. From the results available, it appears that the protandrous cycle is less marked in other members of the Hygrophila, for example, in both *P. gyrina* (De Witt, 1954) and *Lymnaea palustris* (Cheatum, 1951) the male and female systems are fully functional during the winter. Amongst the Stylommatophora, Hickman, (1931) reports that *Succinea ovalis* is a simultaneous hermaphrodite, spermatozoa and ova maturing together in the ovotestis.

Throughout the four families of the Hygrophila, the portion of the vas deferens anterior to the prostate runs, as a general rule, through the musculature of the mantle (see Baker, 1928 and Germain, 1930). It then re-enters the body cavity and joins the penis. In *Pythia* and most tectibranchs, however, there is an open seminal groove which runs from the common genital aperture to the male orifice (Morton, 1955a). In all ellobiids, other than *Pythia*, the vas deferens runs forward from the female opening to the male genital pore as a closed tube, sunk beneath the integument. It seems probable, therefore, that the passage of the vas deferens through the mantle wall represents a relic of the ancestral condition at the ellobiid level of evolution. Furthermore, in the tectibranchs and ellobiids, the penis and anterior vas deferens are separated from the remainder of the genital system. It is of interest in this respect that the reproductive systems of *Lymnaea stagnalis* (Fraser, 1946) and *Physa fontinalis* (Duncan, 1956) develop from three centres. The ovotestis originates from a mesodermal rudiment, whilst the remainder of the genitalia develop from two ectodermal anlagen. One of these gives rise to the female system and most of the male organs, with the exception of the penis and the anterior portion of the vas deferens which differentiate from the third rudiment.

Summing up, therefore, it may be concluded that the genital systems of the

higher Basommatophora illustrate several features reminiscent of the more primitive families of the order.

ACKNOWLEDGMENTS

It is a pleasure to be able to thank Dr J. E. Forrest for his help and valuable criticism and Professor J. E. Morton for his advice and suggestions.

REFERENCES

Baker, F. C. (1928). The freshwater Mollusca of Wisconsin—Pt. I—Gastropoda. *Wisconsin. Acad. Sci. Arts and Letters Monograph*—Bull. No. 70 *Wisconsin geol. nat. Hist. Surv.* (Univ. of Illinois).

Baldwin, E. & Bell, D. J. (1938). Preliminary investigation of galactogen from the albumin glands of *Helix pomatia*. *J. chem. Soc.* **1938** : 1461-5.

Cheatum, E. P. (1951). Effect of temperature-change upon egg production in *Lymnaea palustris* (Muller). *Field & Lab.* **19** : 84-85.

DeWitt, R. M. (1954). Reproductive capacity in a pulmonate snail (*Physa gyrina* Say). *Amer. Nat.* **88** : 159-164.

Duncan, C. J. (1956). *Studies on the reproduction of certain pulmonate gastropods*. Thesis, Univ. of London.

Duncan, C. J. (1958). The anatomy and physiology of the reproductive system of the freshwater snail *Physa fontinalis* (L.). *Proc. zool. Soc. Lond.* **131** : 55-84.

Duncan, C. J. (1959). The life-cycle and ecology of the freshwater snail *Physa fontinalis* (L.). *J. Anim. Ecol.* **28** : 97-118.

Duncan, C. J. (1960a). The genital systems of the freshwater Basommatophora. *Proc. zool. Soc. Lond.* **135** (In press).

Duncan, C. J. (1960b). The anatomy of the reproductive system of *Succinea pfeifferi* Rossmaessler. *Proc. Malacol. Soc. Lond.* (In press).

Fraser, L. A. (1946). The embryology of the reproductive tract of *Lymnaea stagnalis appressa* Say. *Trans. Amer. micr. Soc.* **65** : 279-298.

Fretter, V. (1946). The genital ducts of *Theodoxus*, *Lamellaria* and *Trivia* and a discussion on their evolution in the prosobranchs. *J. mar. biol. Ass. U.K.* **26** : 312-351.

Fretter, V. & Graham, A., (1954). Observations on the opisthobranch mollusc *Acteon tornatilis* (L.). *J. mar. biol. Ass. U.K.* **33** : 565-585.

Germain, L. (1930). Mollusques Terrestres et Fluviatiles. *Faune de France* No. 21.

Hickman, C. P. (1931). Spermiogenesis of *Succinea ovalis* Say., with special reference to the components of the sperm. *J. Morph.* **51** : 243-289.

Holm, L. W. (1946). Histological and functional studies on the genital tract of *Lymnaea stagnalis appressa* Say. *Trans. Amer. micr. Soc.* **65** : 45-68.

Hubendick, B. (1945). Phylogenie und Tiergeographie der Siphonariidae. Zur Kenntnis der Phylogenie in der Ordnung Basommatophora und des Ursprungs der Pulmonatengruppe. *Zool. Bidrag Uppsala* **24** : 1-216.

Hubendick, B. (1947). Phylogenetic relations between the higher limnic Basommatophora. *Zool. Bidrag Uppsala* **25** : 141-164.

Morton, J. E. (1954). Notes on the ecology and annual cycle of *Carychium tridentatum* at Box Hill. *Proc. malacol. Soc. Lond.* **31** : 30-46.

Morton, J. E. (1955a). The evolution of the Ellobiidae with a discussion on the origin of the Pulmonata. *Proc. zool. Soc. Lond.* **125** : 127-168.

Morton, J. E. (1955b). The functional morphology of the British Ellobiidae (Gastropoda, Pulmonata) with special reference to the digestive and reproductive systems. *Philos. Trans.* (B) **239** : 89-160.

Morton, J. E. (1958). *Molluscs*. London.

Quick, H. E. (1933). The anatomy of British Succineae. *Proc. malacol. Soc. Lond.* **20** : 295-318.

Quick, H. E. (1936). The anatomy of some African Succineae and of *Succinea hungarica* Hazay and *S. australis* Ferrusac for comparison. *Ann. Natal Mus.* **8** : 19-45.

SOCIAL BEHAVIOUR AMONG TAME RATS AND AMONG WILD-WHITE HYBRIDS

BY

S. A. BARNETT

Zoology Department, Glasgow University

[Accepted 10th November, 1959]

(With one figure in text)

Social behaviour of wild-white hybrids and of tame albino rats in experimental colonies is compared, with special reference to the intensity of ' social stress ', and contrasted with that of wild rats (described in a previous communication).

CONTENTS

	Page
Introduction	611
Rats and methods	612
Results	613
(a) The colonies	613
(i) Mortality	613
(ii) Growth	614
(iii) Behaviour of hybrids	615
(iv) Behaviour of tame rats	615
(b) Interlopers	615
(c) Adrenal weights	616
(d) Pathology	618
Discussion	618
Acknowledgment	620
Summary	620
References	620

INTRODUCTION

An analysis of the social behaviour of wild rats (*Rattus norvegicus* Berkenhout) has been published (Barnett, 1958a). This study did not deal with the differences between wild rats and laboratory rats (which are of the same species). The most familiar differences in behaviour are in the various components of ' wildness ' and ' savageness ', and these have been discussed in a number of studies (reviewed by Munn, 1950, pp. 98 e.s.). Karli (1956) found that wild rats kill mice more readily than tame rats do. Another behaviour contrast is in the avoidance of strange objects in a familiar situation : this is very marked in wild rats but is not displayed by tame rats (Barnett, 1958d).

Social behaviour among tame rats has been little studied. Munn (1950), in his excellent compilation on the behaviour of tame rats, puts his account of social behaviour in the chapter on abnormal behaviour, and states : ' rats are not essentially influenced by each other's actions '. Tolman (1945) has asserted that rats have ' very little social life '. A few authors have adopted a less naive attitude towards the social behaviour of laboratory rats. Small (1899, 1900) gave some account of social interactions among the rats he studied, but was primarily interested in learning and in the ontogeny of behaviour. Buytendijk (1932) and Soulairac (1952) have published short accounts of laboratory rats

in conditions resembling those in which wild rats live. Most other studies of social behaviour among laboratory rats have involved putting them in highly contrived conditions in order to observe specific forms of response. Seward (1945a, b ; 1946), for example, studied ' fighting ' between males in order to throw light on the development of dominance and subordination as affected by experience of victory or defeat during conflicts of short duration.

The experiments described below were designed to show what sorts of social interactions do occur in colonies of tame rats, and to clarify the differences in social behaviour between tame and wild rats.

RATS AND METHODS

The tame rats were (a) of an albino variety and (b) of a black-hooded variety, both from the Agricultural Research Council, Compton. Neither strain was rigorously inbred in Glasgow. Both are typical laboratory strains, fertile in small cages and easily handled. Also used were hybrid rats derived from a mating between an albino female and a wild male ; the latter had been trapped in Glasgow. The offspring of this cross (the F_1 generation) were, as expected, wild-type in appearance. A single F_1 pair, mated in January 1956, was the origin of the hybrid strain, which is now maintained as a laboratory breeding stock. Colours in the F_2 and subsequent generations have included black, wild-type, black and white, brown and white, various shades of fawn, and white. After several generations, wild-type and fawn predominated. The rats used were of the third or fourth generations, counting the F_1 as the first. They were wild and savage in their behaviour when handled. Details of their management have been given by Barnett (1958c). All the rats, wild or tame, were sexually mature and were between four and eight months old. They were weighed to the nearest 5g. at the start and end of experiment. The body weight ranges are given in table 1.

TABLE 1

Body weight ranges of male rats at the start of experiment, in g.

HYBRIDS		TAME				
Colony members	Controls	Colony members	Albino ' stressed '	Hooded ' stressed '	Albino controls	Hooded controls
200–430	175–435	180–315	270–320	265–285	220–340	240–280

Forty-one hybrid and eighteen albino male rats were studied in colonies in large cages each fitted with five nest boxes. As in the previous study (Barnett, 1958a) the members of colonies were strangers to each other, and to the cage, at the start of the experiment. Each colony consisted of equal numbers of males and females, and was (with two exceptions) maintained for about ten weeks (Table 2). Controls were litter mates of the experimental males, and were kept, each in a small cage, with one female. There were thirty-eight hybrid controls and eighteen albino. In addition to the colony members six hooded males and six albino were ' stressed ' by being added to established albino colonies. Again, litter-mate controls were kept in small cages.

The adrenal glands of most of the males used in these experiments were removed immediately after the rat had been killed, and cleaned of fat. Left adrenals were fixed in Bouin's fluid and right adrenals in formalin calcium ; both were weighed to the nearest 0·1 mg. after fixation for 24 hours.

Behaviour in the colonies was watched for periods of two to three hours in the evenings, at irregular intervals, in order to get a general picture of the range of activities of the rats.

RESULTS

(a) *The colonies*

(i) Mortality

Table 2 gives a list of the colonies and the number of deaths in each. There were no deaths among the females. Of the controls, two wild-type hybrid males died. The most obvious feature of the mortality was the difference between the hybrid and the albino rats. Eighteen of the latter were made up into three colonies, and none died ; of thirty-one hybrid males from nine colonies each maintained for ten weeks, twelve died. Two other colonies of hybrid rats (nos 41 and 48) were maintained for only two and three weeks respectively ; of the ten males in these, only one died.

TABLE 2

The experimental colonies.

Colony no.	Duration : weeks	Rats				Deaths of ♂s
		Wild type	Other hybrid	Tame (albino)	♀s	
35	10	—	4	—	4	0
37	10	4	—	—	4	3
38	10	—	4	—	4	0
39	10	3	—	—	3	2
44	10	1	5	—	6	4
46	10	1	3	—	4	3
51	10	2	4	—	6	0
41	2	6	—	—	6	0
48	3	2	2	—	4	1
23	10	—	—	6	6	0
50	9	—	—	6	6	0
52	9	—	—	6	6	0

A question arising from the mortality figures was whether there was a tendency for more deaths to occur in colonies with wild-type males. Of the seven hybrid colonies each lasting ten weeks, two (nos 37 and 39) contained only wild-type males ; in each of these only one remained at the end. Two colonies (nos 35 and 38) contained no wild-type males, and in these no deaths occurred. The remaining three contained both wild-type and other hybrid males : in them

the deaths were respectively four out of six (expt. 44), three out of four (expt. 46) and none out of six (expt. 51). In each of experiments 44 and 46 there was only one wild-type male, and both of these died.

Just as in the experiments with wild rats, the hybrid rats died without being severely wounded. The question of the cause of death in these conditions has been discussed elsewhere (Barnett, 1958b ; Barnett, Eaton & McCallum 1960).

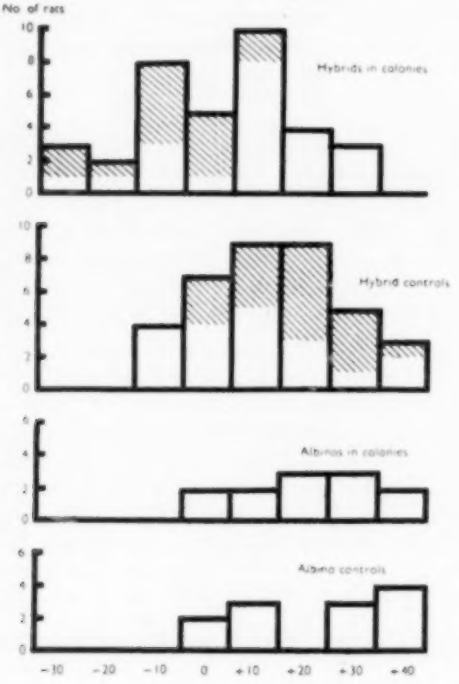


Fig. 1.—Distribution of percentage change in body weight per ten weeks, in hybrid and in tame albino males kept in colonies, and in the corresponding control rats kept in small cages. In the upper two histograms the hatched areas represent the wild-type males ; the latter tended to lose weight in the colonies more than the males of other colour varieties. The top histogram is incomplete, since six colony members died during the experiments and were partly eaten before they could be weighed. These rats, of which four were wild-type, would have appeared on the left hand of the histogram.

(ii) *Growth*

The differences between the three classes of rats, namely, wild-type hybrids, other hybrids and tame albinos, were further illustrated in the changes in body weights (Fig. 1). Most of the *tame rats* grew substantially, and none lost weight; there was no evident difference between those in colonies and the controls. Most of the *hybrid controls* gained in weight also. By contrast, many of the *hybrid colony members* lost weight ; among them, the wild-type males tended to lose weight more than the other hybrids. In Fig. 1 only thirty-five rats

are represented in the histogram for hybrid colony members. Six others were not weighed because they died before the experiment ended and had been partly eaten before they were found. All the rats that died during the experiments, and that were weighed, had lost weight ; consequently the histogram is misleading in that six rats, which should have appeared among those that lost weight, are omitted ; of these six, four were of the wild type.

(iii) *Behaviour of hybrids*

The behaviour of wild *Rattus norvegicus* in artificial colonies has been described elsewhere (Barnett & Spencer, 1951 ; Barnett, 1958a, b). The behaviour of the hybrid males in the present experiments did not differ qualitatively from that of wild males. On the setting up of a colony there was the usual extensive exploration, both of the strange cage and of other rats. Conflict between males developed, in some instances, within a few minutes, but the females did not fight. Males displayed all the components of fighting observed in wild rats, including tooth chattering, threat posture, jumping and biting ; ' amicable ' behaviour, similar to that of wild rats. also occurred, including ' crawling under ', mutual grooming and the ' submissive posture '.

(iv) *Behaviour of tame rats*

The albino rats displayed the expected high intensity of exploratory behaviour on being put in the unfamiliar cage. There was much sniffing of other rats ; the males also inspected the genitals of the females, and pursued females which ran away. Some scuffling developed among the males soon after the colonies were set up, but no biting was seen ; nor was there any evidence of it later, since no injuries were seen among colony members. The most marked difference from wild and hybrid rats was in the absence of certain specific behaviour patterns : there were no tooth chattering, threat posturing or vigorous leaping or biting in attack, such as are found among wild rats ; nor was there any amicable crawling under.

b. *Interlopers*

Of the twelve males, six albino and six hooded, added to established albino colonies, none died. Of the ten of which the weights were recorded, eight lost weight during the eight days of the experiment. Only two controls lost weight (Table 3). One control rat, no. w3, lost much weight, as did its brother which was one of the experimental animals ; these two were evidently in poor condition, but the cause of this was not discovered.

The behaviour which followed introduction of strange rats into a colony is best presented by an example.

Colony no. 50. Two hooded males ' B ' and ' N ' (285 and 270 g. respectively) are put in together. Both explore and enter nest boxes without opposition. A large male X, (>285 g.), sniffs B, partly as if B were female, and grooms B while B keeps still. The same with N. X tries coitus with B; scuffle and squeal but no real fight. A female comes out, ignores B and N, is sniffed by X. N sits in corner as if rather shocked, after encounter with X, breathing jerky and slow. B settles in a nest box.

TABLE 3

Weight changes of 'stressed' rats and controls.

Rat no.	'Stressed'			Controls		
	Initial wt. g.	Final wt. g.	% change	Initial wt. g.	Final wt. g.	% change
h1	285	270	−5	240	275	+15
h2	270	240	−11	260	290	+12
h3	265	285	+7	240	270	+13
h4	275	250	−9	280	305	+9
w1	270	250	−7	280	270	−4
w2	270	280	+4	250	255	+2
w3	320	220	−31	310	225	−27
w4	350	320	−9	340	360	+6
w5	330	325	−2	320	370	+9
w6	270	235	−13	310	315	+2

The period of the experiment for each rat was eight days. Controls were litter mates of the stressed rats; h = hooded; w = albino. Two other hooded rats were stressed, but their weights were not recorded.

Female grooms N. X attempts coitus with N, and bites N on failing. N is pursued by X; X licks N's genitals whenever possible. N attempts flight whenever approached by X, and shows signs of shock again. Twenty minutes after start, N enters a nest box, is pursued by X and prevents X from getting in. Later, X succeeds, but no scuffle follows. X keeps on going in and out of nest box.

This example is one of a vigorous response of a tame resident male to interlopers. On other occasions such encounters were less eventful, and the ambivalent response, partly as though the newcomers were female, was not seen. In every instance the newcomers eventually settled down and slept among a group of both sexes in a nest box (or, in one instance, on the floor of the cage); their behaviour soon became indistinguishable from that of other colony members. A notable difference from wild rats on being put in a strange cage was in feeding behaviour; tame rats sometimes began to eat within one hour of introduction into the cage, whereas wild rats in these conditions do not eat for many hours or even days (Barnett & Spencer, 1953).

c. *Adrenal weights*

The adrenal glands were weighed because an increase in adrenal weight is an index of 'stress'. Table 4 summarizes the data. For reasons given by Barnett (1958b) both absolute and relative weights are shown. The hybrid males in the colonies had heavier adrenals than the controls. The adrenals of the rats that died were not weighed, andthe mean adrenal weight for colony members (64 mg.) therefore does not represent the whole class, but only survivors. The rats that died must have been those most affected by the 'social stress' in the colonies, and it is just these rats that would be expected to have the

TABLE 4

Adrenal weights.

		No. of rats	Mean adrenal weight	
			mg.	mg./100 g.
Hybrids	colony members	22	64·4±4·31*	21·1±1·66**
	controls	31	53·9±3·52	17·1±1·17
Tame	colony members (albinos)	11	34·6±3·42**	11·9±0·64**
	albino 'stressed'	6	28·0±2·98	10·8±1·58*
	hooded 'stressed'	4	32·6±1·02	12·5±0·70
	albino controls	18	25·3±1·52***	8·0±0·45***
	hooded controls	4	33·6±1·09	11·8±0·08

*significantly different from controls ($P < 0·05$)
**significantly different from controls ($P < 0·01$)
***significantly different from hooded ($P < 0·01$)
In this and the following table each mean is followed by its standard error.

largest adrenals ; hence the difference between colony members and controls, shown in the table, is probably less than it should be. These observations parallel those made on unmixed wild rats (Barnett, 1958b), but the adrenals of the hybrid males were lighter than those of wild males (Table 5).

Albino colony members too had adrenal glands heavier than those of the albino controls (Table 4). It is well known that the adrenals of tame rats are lighter than those of wild rats (Donaldson, 1924 ; Rogers & Richter, 1948). The adrenals of the albino controls of the present experiments were less than

TABLE 5

Comparison of adrenal weights of male hybrid and wild rats.

	Controls			Members of ♂ and ♀ colonies		
	No. of rats	mg.	mg./100 g.	No. of rats	mg.	mg./100 g.
Hybrids	31	53·9±3·52	17·1±1·17	22	64·4±4·31	21·1±1·66
Wild	15	60·0±4·09	20·7±1·46	15	82·5±5·32	30·3±2·43

Data on wild rats taken from Barnett (1958b).

half the relative weight of the adrenals of wild rats kept in the same conditions ; and the difference between colony members of the two classes of rat was still greater.

Table 4 also gives data on the adrenals of tame males ' stressed ' by being put in established colonies. When this procedure is adopted with wild rats, a marked enlargement of the adrenals follows (Barnett, 1958b). In the same way, the six stressed albino males had a mean relative adrenal weight significantly higher than that of the controls ; but the four stressed hooded rats of which the adrenal weights were recorded showed no such effect. The hooded rats had larger adrenals than the albinos. The latter observation has been confirmed on much larger numbers of rats (unpublished), and is an example of the genetical variation in adrenal weights in different strains already reported by Yeakel & Rhoades (1941).

d. *Pathology*

The general appearance of all the rats at the beginning of these experiments was healthy. The stocks from which they were drawn breed and grow well, and there is little unexplained mortality. Some of the hybrid rats, and some of the wild rats of the stock from which the hybrids were partly derived, have been given a routine pathological examination after being killed. The results have been published elsewhere (Barnett, Eaton & McCallum, 1960) : the main finding was the presence of mild chronic murine pneumonia in many of the rats. This is often present in laboratory rat colonies.

Four hooded males, of which two were controls and two were ' stressed ', used in the present experiments, were examined after death : the kidneys, intestines, liver, spleen and adrenal glands were all normal on microscopical examination after routine staining ; the lungs of all four showed mild chronic murine pneumonia. Previous unpublished observations on members of the albino rat stock had shown that this disease was also present among them.

DISCUSSION

The behaviour of the *hybrid* males in the colonies did not differ materially from that of wild rats : the patterns of attack and of amicable behaviour were the same ; there was a substantial death rate attributable to ' social stress ' ; and among the surviving rats there was a tendency, similar to that found in wild rats, for growth to be reduced and for the adrenal glands to enlarge. However, none of the hybrid rats displayed the extremes of aggression observed in a few of the wild males (Barnett, 1958a). It is likely that detailed quantitative study would show that the ' average social aggressiveness ' of hybrids is lower than that of wild males, just as Stone, Darrow, Landis & Heath (1932) found that wild-white hybrids were intermediate between the parent strains in wildness.

Behaviour is evidently sometimes associated with coat colour, as Keeler & King (1942) suggest (cf. Broadhurst, 1958). In particular, wild-type hybrid males tended to resemble wild males both in their behaviour and in their response to social stress, as well as in appearance. But such a relationship between wildness or social aggression on the one hand, and coat colour on the

other, does not hold among laboratory strains : the wild-behaving hybrids used in the present experiments included albino, piebald and black rats, that is, rats with coat colours which are also to be found among completely tame laboratory varieties.

The expression ' completely tame ' contains the implication that there is a scale of tameness, and that laboratory rats score the maximum number of points on this scale. The technique of assessing tameness quantitatively has been discussed by Munn (1950, pp. 98 e.s.). Here we may note that laboratory rats, such as the albino and hooded rats used in the present experiments, usually show in their responses to man only one faint trace of their wild ancestry : they do walk away when one tries to pick them up. An important question is : are laboratory rats equally free from the aggressive behaviour patterns which wild males direct towards other males of their own species? It is clear, both from the experiments described above and from previous work such as that of Seward (1945a, b, 1946), that tame rats retain some social aggressiveness. The present experiments showed also that this is most clearly displayed when a male, already established in a living space, encounters a strange male ; in this too, tame rats resemble wild ones. Nevertheless, the tame rats of these experiments wholly lacked some of the most conspicuous stereotyped components of the fighting of wild rats : in particular, the ' threat posture '. Further, they lacked one of the most distinctive patterns of amicable behaviour, namely, ' crawling under '. Much of the behaviour of the tame rats that would ordinarily be called ' fighting ' was of a different character from that of the intense conflict between wild males. As Grant & Chance (1958) have pointed out, it resembles the play of immature rats. It is also similar to the ' fighting ' seen among wild *females*, and to that of adult litter mates brought up together (Barnett, 1958a).

Despite the low intensity of the conflict among tame male rats it does have measurable physiological effects such as are seen also among wild rats. The albino rats, both those of the experimental colonies and those put as strangers into established colonies, had larger adrenal glands than the controls (Table 4) : this may be regarded as an index of some degree of ' social stress ' (Barnett, 1958b). Further, the growth of the interlopers was interrupted (Table 3). The interruption of growth might be attributed to the mere disturbance of transfer to a new cage (Steinberg & Watson, 1960) ; but since it did not occur in the colony members, this seems unlikely. It seems likely that laboratory rats, with their small adrenals, are less able to withstand various sorts of ' stress ' than wild rats : the mean weight of the adrenals of albino colony members was about 40 per cent above that of albino controls, while the corresponding figure for both wild and hybrid males was only about 20 per cent. The adrenals of albino controls weighed about 40 per cent of those of wild controls ; and those of albino colony members about 40 per cent of wild colony members. No doubt, however, more severe ' stress ' would have induced the albino adrenals to enlarge further.

To sum up, the artificial selection to which laboratory rats have been subjected for more than half a century has produced varieties which differ behaviourally from wild rats in the following respects :

(i) some components of fighting and amicable behaviour have been totally lost ;
(ii) the remaining fighting behaviour tends to be immature in character and is almost harmless;
(iii) wildness and savageness towards man have been almost wholly lost ;
(iv) fear of new objects in a familiar environment has been lost.

The rat, in fact, treated as a whole animal and not only as a ' furry test-tube ', provides unusual opportunities for the study of the effects of genetical variation, selection and the interactions of nature and nurture on behaviour.

ACKNOWLEDGMENT

Grateful acknowledgment is due to Raymond Stoddart and John Keys for technical help.

SUMMARY

Adult albino laboratory rats (*Rattus norvegicus* Berkenhout) were put together in colonies in large cages, in conditions which lead to severe conflict and death among wild rats of the same species. There were no deaths and little conflict. Hybrid rats, obtained from an albino-wild cross, were similarly treated. These responded in the same way as unmixed wild rats, though with conflict of lower intensity. Wild-type hybrid males were probably more combative, and more susceptible to ' social stress ', than hybrid males of other colours.

The albino rats lacked most of the repertoire of aggressive and ' amicable ' social signals which are found in wild rats.

Male albino and hooded rats were put into established colonies of albino rats. In these conditions wild males make fierce and usually lethal attacks on interlopers. The resident albinos made only mild attacks ; no deaths occurred and the interlopers were absorbed into the colonies.

The adrenal glands of male members of colonies, controls kept in small cages and of interlopers were weighed. Colony members, whether tame albino or hybrid, had heavier adrenals than the corresponding controls. This indicated that even among the albinos membership of a colony involved some ' social stress '. Albino interlopers also had enlarged adrenals.

The behavioural changes which have resulted from the selection of laboratory rats for tameness are discussed.

REFERENCES

Barnett S. A. (1958a). An analysis of social behaviour in wild rats. *Proc. zool. Soc. Lond.* **130** : 107-152.

Barnett, S. A. (1958b). Physiological effects of ' social stress ' in wild rats—1. The adrenal cortex. *J. Psychosom. Res.* **3** : 1-11.

Barnett, S. A. (1958c). Laboratory methods for behaviour studies of wild rats. *J. anim. Tech. Ass.* **9** : 6-14.

Barnett, S. A. (1958d). Experiments on ' neophobia ' in wild and laboratory rats. *Brit. J. Psychol.* **49** : 195-201.

Barnett, S. A., Eaton J. C. & McCallum, H. M. (1960). Physiological effects of ' social stress ' in wild rats—2. Liver glycogen and blood glucose. *J. Psychosom. Res.* (in press).

Barnett, S. A. & Spencer, M. M. (1951). Feeding, social behaviour and interspecific competition in wild rats. *Behaviour* **3** : 229-242.

Barnett, S. A. & Spencer, M. M. (1953). Experiments on the food preferences of wild rats (*Rattus norvegicus* Berkenhout). J. *Hyg., Camb.* **51** : 16-34.

Broadhurst, P. L. (1958). Determinants of emotionality in the rat : 3. Strain differences. *J. comp. physiol. Psychol.* **51** : 55-59.

Buytendijk, F. J. J. (1931). Eine Methode zur Beobachtungen von Ratten in aufgabefreien Situationen. *Arch. Néerl. Physiol.* **16** : 574-596.

Donaldson, H. H. (1924). *The rat.* Philadelphia.

Grant, E. C. & Chance, M. R. A. (1958). Rank order in caged rats. *Anim. Behav.* **6** : 183-194.

Karli, P. (1956). The Norway rat's killing response to the white mouse : an experimental analysis. *Behaviour* **10** : 81-103.

Keeler, C. E. & King, H. D. (1942). Multiple effects of coat color genes in the Norway rat, with special reference to temperament and domestication. *J. comp. Psychol.* **34** : 241-250.

Munn, N. L. (1950). *Handbook of psychological research on the rat.* New York.

Rogers, P. V. & Richter, C. P. (1948). Anatomical comparison between the adrenal glands of wild norway, wild alexandrine, and domestic norway rats. *Endocrinology* **42** : 46-55.

Seward, J. P. (1945a). Aggressive behaviour in the rat. I. General characteristics ; age and sex differences. *J. comp. Psychol.* **38** : 175-197.

Seward, J. P. (1945b). Aggressive behaviour in the rat. 2. An attempt to establish a dominance hierarchy. *J. comp. Psychol.* **38** : 213-224.

Seward, J. P. (1946). Aggressive behaviour in the rat. 4. Submission as determined by conditioning, extinction and disuse. *J. comp. Psychol.* **39** : 51-75.

Small, W. S. (1899). Notes on the psychic development of the young white rat. *Amer. J. Psychol.* **11** : 133-165.

Small, W. S. (1900). An experimental study of the mental processes of the rat. *Amer. J. Psychol.* **11** : 133-165

Soulairac, A. (1952). In *Structure et Physiologie des Sociétés des Animals.* Paris.

Steinberg, H. & Watson, R. H. J. (1960). Failure of growth in disturbed laboratory rats. *Nature, Lond.* **185** : 615-616.

Stone, C. P., Darrow, C. W., Landis, C. & Heath, L. L. (1932). In *Studies in the dynamics of behaviour.* Chicago.

Tolman, E. C. (1945). A stimulus-expectancy need-cathexis psychology. *Science, N.Y.* **101** : 160-166.

Yeakel, E. H. & Rhoades, R. P. (1941). A comparison of the body and endocrine gland (adrenal, thyroid and pituitary) weights of emotional and non-emotional rats. *Endocrinology* **28** : 337-40.

THE MORPHOLOGY OF *BRUMPTIA BICAUDATA* (POIRIER, 1908) ODHNER, 1926 (TREMATODA : PARAMPHISTOMOIDEA)

BY

SHEILA WILLMOTT

*Institut de Zoologie, Université de Neuchâtel**

[Accepted 10th November 1959]

(With 9 figures in the text)

Brumptia bicaudata is redescribed and redefined, with particular reference to the genital organs, hermaphroditic pouch and genital papilla. A ciliated valve which separates the vesicula seminalis and ejaculatory duct is described ; the ejaculatory duct is lined with ciliated epithelium. The subfamily Brumptinae is redefined.

CONTENTS

	Page
Introduction	623
Anatomy of male organs	625
Anatomy of female organs	630
Anatomy of hermaphroditic pouch and genital papilla	631
Discussion	632
Taxonomic position	632
Acknowledgments	633
References	633
Key to lettering of text figures	633

INTRODUCTION

Brumptia bicaudata was first described by Poirier in 1908 (although the actual date of publication of the description appears to be 1909) as *Amphistomum bicaudatum* from specimens collected from the African elephant. In his description he noted the pair of extraordinary caudal appendages, which he considered acted as organs of adhesion accessory to the ventral sucker, and the presence of an almost spherical cirrus pouch. In 1917 MacCallum described *Cladorchis gigas* from material collected by the American Museum of Natural History Expedition to the Belgian Congo and drew attention to the very large cirrus sac. Travassos, in 1921, erected the genus *Brumptia* for *C. gigas* MacCallum, 1917 and based the generic diagnosis on the caudal appendages and the presence of a cirrus sac and a genital sucker. In 1923 Maplestone gave a very detailed account of the anatomy of *B. gigas* from two collections from the rhinoceros and illustrated it with diagrams of sections and photographs of whole specimens, one of which showed the genital papilla extruded.

Stunkard proposed, in 1925, the erection of a new subfamily, the Brumptinae, for this genus but gave no diagnosis, simply stating " with the characters of the genus " and this subfamily has been generally accepted ; in 1949

*On leave from the Commonwealth Bureau of Helminthology, St. Albans, Herts.

Skryabin raised the Brumptinae to family rank in the superfamily Cladorchoidea of the order Paramphistomata but it seems doubtful that this is justified on the basis of our present knowledge. In 1926 Stunkard and Odhner, both independently, drew attention to the identity of *Amphistomum bicaudatum* and *Cladorchis gigas* and showed that on the grounds of priority the correct name for this parasite was *Brumptia bicaudata*. In 1929 Stunkard published a redescription of *B. bicaudata*, based on an examination of Poirier's material and of that from the Belgian Congo Expedition, in which he quoted Poirier's original description in full. The cirrus pouch was again especially noted and the presence of a receptaculum seminis uterinum reported for the first time. Fukui, in 1929, suggested that the term " hermaphroditic pouch " should be

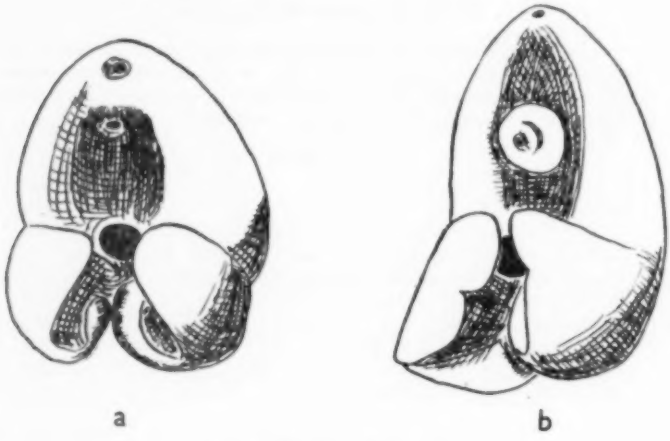


Fig. 1.—*Brumptia bicaudata*.
(a) from African Elephant, with invaginated genital papilla. (Length 12 mm., maximum breadth 10 mm.)
(b) from Rhinoceros, with evaginated genital papilla. (Length 13 mm., maximum breadth 8 mm.)

substituted for " cirrus pouch " as both male and female ducts were contained in it and gave a brief diagnosis of the subfamily Brumptinae. Apart from a very short account by Näsmark in 1937, in which he aligned the Brumptinae with the Gastrodiscidae rather than with the Paramphistomidae, little further attention has been paid to this amphistome.

From examination of specimens in the collections in the Institut de Zoologie, Université de Neuchâtel, in the Liverpool School of Tropical Medicine, and in the British Museum (Natural History) it is now shown that the organ hitherto regarded as a cirrus pouch or, more accurately, as a hermaphroditic pouch is also the invaginated genital papilla, and that the so-called genital sucker is not a muscular sucker in the usual sense of the word but is a compact mass of lymph canals, bordered by some muscular tissue, which surrounds the opening through which the genital papilla evaginates.

According to Maplestone the genital papilla appeared as a long muscular tube, the cirrus pouch was a spherical organ about 4 mm. in diameter having the wall composed of loosely laminate muscle fibres, and the genital pore was provided with a definite small sucker. Comparison of sagittal sections of specimens in which the genital papilla has remained invaginated with the drawings of similar sections which were given by Maplestone shows general agreement in the arrangement but considerable differences in interpretation : had Maplestone cut sections of the specimen in which the genital papilla had evaginated his conclusions might well have been very different. In view of these observations a redescription of the genital organs of *Brumptia bicaudata* appears to be necessary and is given below.

ANATOMY OF MALE ORGANS

The testes are, as recorded in the earlier descriptions, very large and divided into a great number of small lobes, most closely resembling a mulberry in appearance. They lie laterally and slightly ventrally to the hermaphroditic pouch and extend from about its midline almost to the acetabulum, abutting the wall of the pouch very closely.

Each vas efferens arises directly from a centrally situated lobe of the testis, coils on itself slightly and expands to form a large thin-walled tube which runs inwards towards the dorsal wall of the pouch. The actual point of union of the two vasa efferentia is still uncertain. Maplestone considered that they joined immediately within the pouch. Stunkard (1929) implied that they united outside the pouch forming a vesicula seminalis which lay partly within and partly without the pouch, but did not remark on the fact that the " cirrus " pouch also contained the uterus. The present observations indicate that the vasa efferentia unite either immediately outside the wall or while actually passing through it. At this point the duct narrows and is very convoluted.

The vas deferens within the pouch is divided into three very distinct regions. The first is a voluminous, thin-walled vesicula seminalis which runs anteriorly, closely applied to the dorsal wall of the pouch ; when this reaches almost to the anterior pole of the pouch it passes into the second, or valve, region. This is a short duct, considerably narrower in diameter than the vesicula seminalis ; the walls of this duct contain very well marked circular muscles and are lined with columnar cells with large, prominent nuclei, and long, strongly developed cilia on their free borders protruding into the lumen ; at the distal end of the duct there is a well developed true sphincter which projects into the third or ejaculatory region and forms the valve proper. From the ejaculatory duct end of the sphincter there arises a hollow cylinder of large cells, also with prominent nuclei, which have tree-like branching processes, all of which are covered with strong cilia, the whole forming a peculiar brush-like apparatus. From the tip of this apparatus to the junction with the vesicula seminalis is about 0·45 mm. to 0·5 mm.; the diameter of the duct is about 0·1 mm. (Fig. 2). From here the ejaculatory duct turns abruptly and runs through the pouch to the male pore. The ejaculatory duct is lined with ciliated epithelium, but the cells are not of the columnar type observed in the valve region, and is surrounded by a thick layer of myoblasts and lymph canals forming the region termed pars

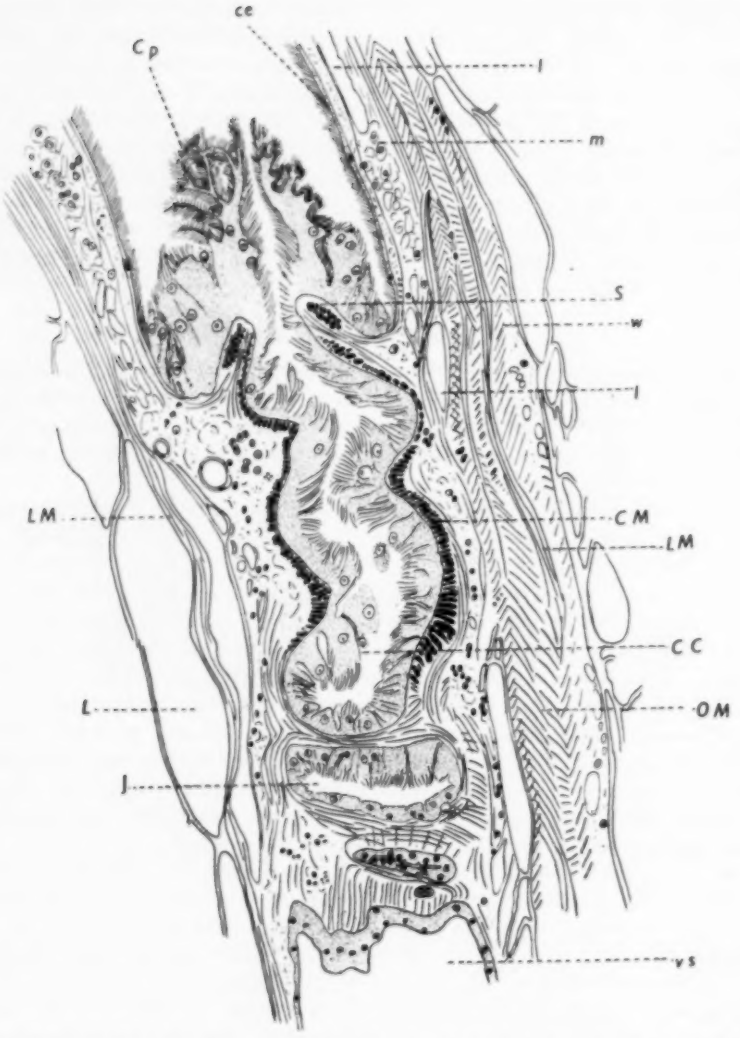


Fig. 2.—Brumptia bicaudata (from African Elephant). Sagittal section of valve in male duct. (15μ.) (Key to lettering, p. 633)

prostatica by Maplestone. But these cells are not glandular although they have large nuclei. The layer of myoblasts and lymph canals is in turn surrounded by a layer of irregularly arranged muscle strands, but does not form a definite pars musculosa. About 1 mm. from the male opening the lining becomes cuticular. These two parts can be seen in the transverse sections of the evaginated genital papilla. (Figs. 3 and 4).

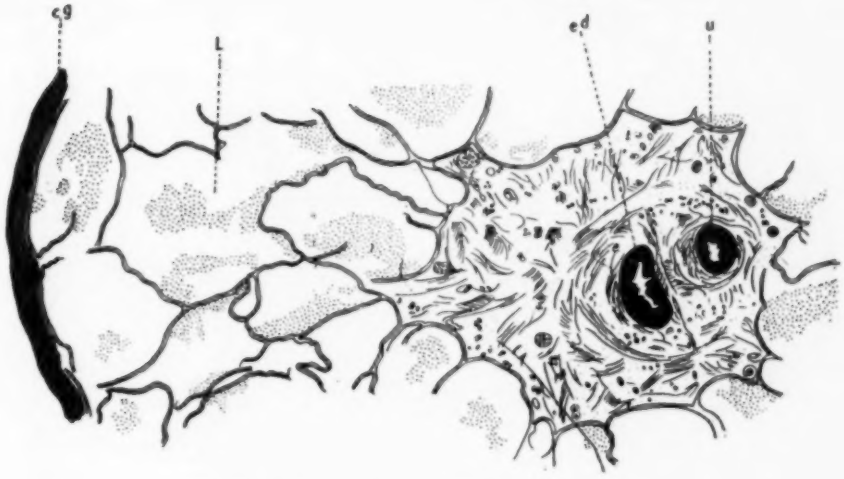


Fig. 3.—*Brumptia bicaudata* (from Rhinoceros).
Transverse section of evaginated genital papilla just below the openings of the ducts to the exterior. (5μ.) (Key to lettering, p. 633)

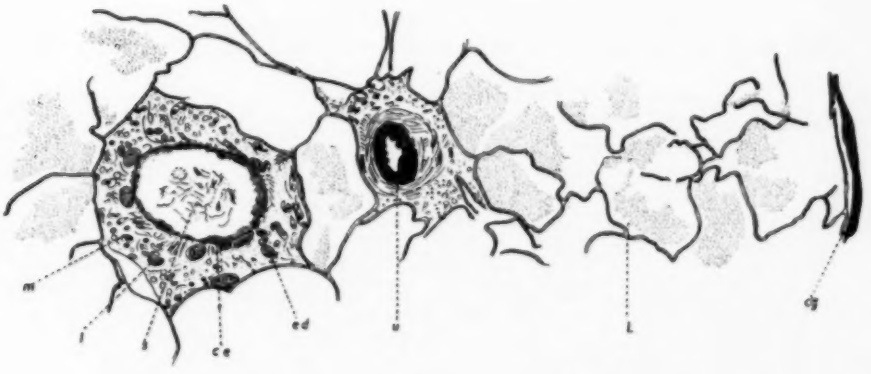


Fig. 4.—*Brumptia bicaudata* (from Rhinoceros).
Transverse section of evaginated genital papilla further from the openings of the ducts. (5μ.)
(Key to lettering, p. 633)

This is believed to be the first time that such a complicated valve structure has been observed and the first record of cilia in the ejaculatory portion of the male duct in this group. Although the presence of cilia in the vasa efferentia has been considered to be characteristic of the paramphistomes, they were not observed in the vasa efferentia in *Brumptia bicaudata*.

The relationships of the various parts of the male duct are best seen in the figures showing sagittal sections of specimens with the genital papilla invaginated and evaginated. (Figs. 5, 6, 7 and 8.)

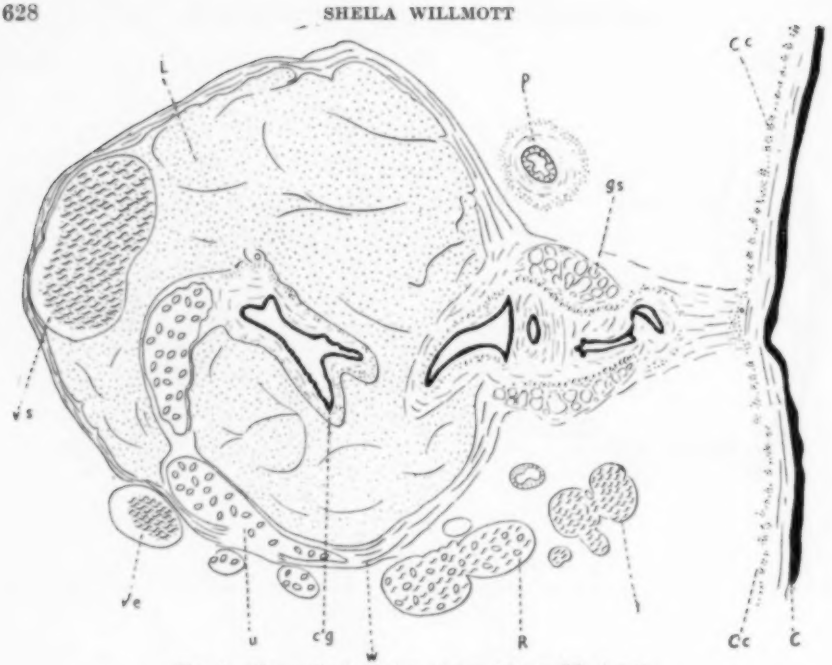


Fig. 5.—*Brumptia bicaudata* (from African Elephant).
Sagittal section of hermaphroditic pouch showing uterus. (15μ.) (Key to lettering, p. 633)

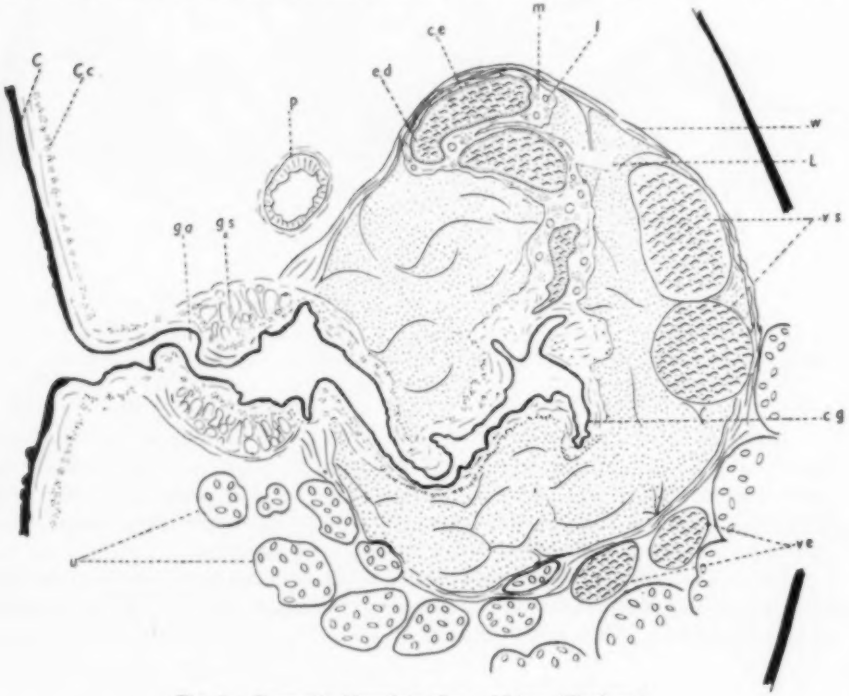


Fig. 6.—*Brumptia bicaudata* (from African Elephant).
Sagittal section of hermaphroditic pouch showing male duct. (15μ.) (Key to lettering, p. 633)

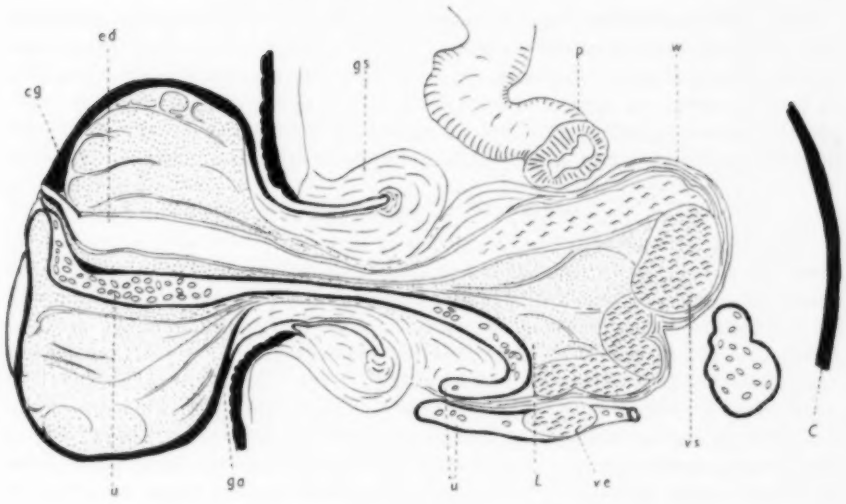


Fig. 7.—*Brumptia bicaudata* (from African Elephant).
Sagittal section of evaginated genital papilla showing both male and female ducts. (Thick hand section.) (Key to lettering, p. 633)

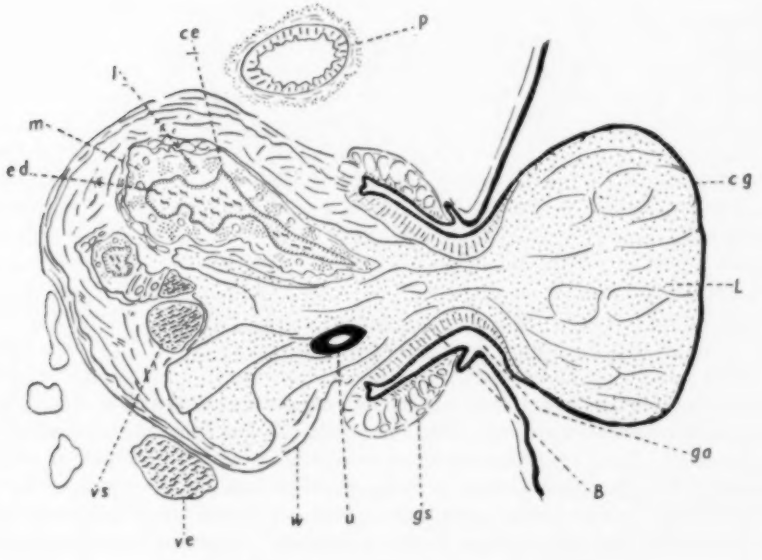


Fig. 8.—*Brumptia bicaudata* (from Rhinoceros).
Sagittal section of evaginated genital papilla showing retention of vesicula seminalis within the hermaphroditic pouch. (15μ.) (Key to lettering, p. 633)

MacCallum described the presence in the vas efferens and the proximal part of the vas deferens (vesicula seminalis) of spermatogonia and spermatocytes in all stages of spermatogenesis and the present observation confirms this. Indeed in some specimens spermatoctyes and developing spermatids were present in considerable numbers amongst the spermatozoa throughout the whole length of the vesicula seminalis and ejaculatory duct. (Figs. 4, 6 and 8.)

ANATOMY OF FEMALE ORGANS

The arrangement of the female genitalia appears to be much as has already been described, but the smooth ovary is subdivided into lobes internally and there are numerous very large lymph canals running through the thin layers of connective tissue which protrude into the ovary itself. (Fig. 9.) The ovary and Mehlis' gland lie close together between the most posterior tips of the testes ; the oviduct is short. The uterus, in gravid specimens, is much convoluted and packed with eggs ; it runs first posteriorly to the level of the acetabulum and excretory bladder and then extends anteriorly, passing behind the hermaphroditic pouch, as far forwards as its anterior border ; here it turns and runs backwards along the dorsal side of the pouch, turns ventrally at its posterior end and passes almost to the ventral surface where it doubles

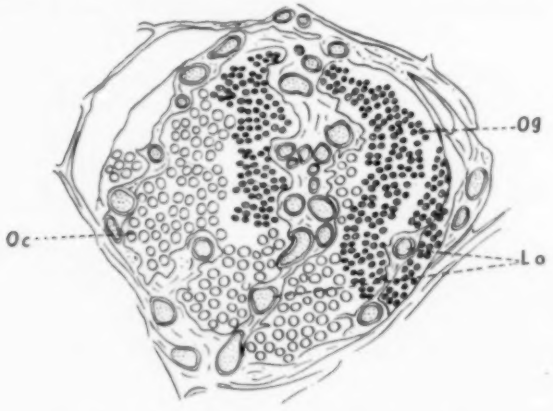


Fig. 9.—*Brumptia bicaudata* (from African Elephant).
Sagittal section of ovary. (15 μ.) (Key to lettering, p. 633)

back and enters the pouch towards the dorsal side at the posterior end. Within the pouch it passes, with very little convolution, directly to the female opening. There is no ductus hermaphroditicus. (Figs. 5 and 7.) There is, as was described by Stunkard (1929), a receptaculum seminis uterinum. The part of the uterus, or metraterm, within the pouch is muscular and that part which is everted in the genital papilla is lined by cuticula. There is no distinct vagina.

In all the specimens from the elephant which were examined the uterus was packed with eggs but this was not the case in Maplestone's two collections from the rhinoceros. The specimens in these two collections were markedly

different in size and both were in rather a poor state of preservation. A few eggs were present in the uteri of those worms which were examined from the lot of small-sized specimens but not in those of the larger worms, although Maplestone had reported gravid ones in both collections. Whether or no this is due to partial or complete sterility in an abnormal host, or to the material being kept overlong in water before fixation so that the eggs were shed is difficult to determine.

The two main vitelline ducts are large in diameter and run along the dorsal side of the caudal alae, around the acetabulum, to unite close to Mehlis' gland which they enter from the posterior side without forming a pronounced vitelline reservoir. A number (usually about five or six) of subsidiary ducts, which may branch, run through the vitelline follicles on each side and join the main vitelline duct approximately at right angles.

ANATOMY OF HERMAPHRODITIC POUCH AND GENITAL PAPILLA

The genital atrium is exceptionally deep. As previously stated, the " genital sucker ", which probably acts as a sphincter closing the atrium during self-fertilization, should be more correctly termed " genital sphincter " because it is almost entirely composed of lymph channels, with a thin muscular layer forming the border, and a comparatively small number of longitudinal and circular muscles continuous with those of the rest of the body wall, towards its internal surface. (Figs. 5 and 6.)

The genital papilla is curious. According to Fukui this, in the amphistomes, is muscular—" a cylindrical muscular elevation of the wall of the atrium "—but in *Brumptia* muscles are almost completely absent from the main part of the evaginated papilla and only poorly developed, in the form of a thickening of the body wall, at its base. When invaginated to form the hermaphroditic pouch it occupies almost the entire width and depth of the body for about a quarter of its length. It is roughly spherical but slightly flattened where the testes press against the wall ; the antero-posterior diameter is approximately 4 mm. and from the dorsal wall of the pouch to the ventral body wall, including the atrium is approximately 6·5 mm. When evaginated the former is about 3·25 mm. and from the dorsal wall of the pouch to the ventral wall of the papilla is about 6·75 mm. ; its diameter at the narrowest part is 1·0 mm. The internal wall, which is not evaginated, is composed of layers of oblique and longitudinal muscles. That part which is evaginated, and forms the external wall, is almost wholly cuticular. The lumen is filled with lymph canals arranged in a manner which recalls that of the segments of an orange, with the external wall and the base of the genital atrium at the centre. It seems likely that pressure within these canals plays a large part in bringing about evagination and that the muscles of the ducts themselves act as retractors. Evagination does not affect that part of the vas deferens and vesicula seminalis which is closely applied to the dorsal wall of the genital papilla or hermaphroditic pouch. (Figs. 7 and 8.)

The wall of the atrium is cuticular with muscles arranged much as in the rest of the body wall. That part which was considered by Maplestone to be the ductus hermaphroditicus becomes the external covering of the evaginated papilla and is entirely cuticular.

DISCUSSION

Although this study is mainly concerned with the structure and arrangement of the genital organs, a number of other points on interest have been noted. The caudal alae do not appear to be very muscular although the previous descriptions have indicated that they were ; they contain almost all the vitelline follicles and a large number of lymph canals but the muscles appear to be similar in arrangement and development to those of the rest of the body wall and certainly do not show the degree of development which would be expected in organs of adhesion; however, only observations on the worms *in vivo* could clarify this question.

The lymph system seems to be exceptionally well developed, particularly in connection with the genital papilla and hermaphroditic pouch and with the ovary and testes, but could not be studied in detail. Neither the excretory system nor the nervous system was investigated, although in the sections of the specimen from the material loaned by the British Museum (Natural History) comparatively thick-walled excretory ducts were observed amongst the layer of cells, in the body wall, which secrete the cuticula.

TAXONOMIC POSITION

The affinities of this bizarre fluke are not all at clear, but on the form and arrangement of the gut with its pharyngeal diverticula, characters regarded by Poirier as being very important distinguishing features, it seems better to align it for the time being with the Gastrodiscidae rather than with the Paramphistomidae. If and when other members of the subfamily or genus are described the erection of a separate family will probably be justified. In any case a thorough practical re-examination of the whole group of amphistomes would be necessary before any definite and authoritative conclusions could be reached. The existing confusion throughout the entire superfamily following Maplestone, who went to one extreme in " lumping ", and Näsmark, who went to the other in " splitting ", will persist until a complete reinvestigation can be undertaken. For the present it is proposed to redefine the subfamily as follows :

Paramphistomoidea : Gastrodiscidae : Brumptinae : characterized by the possession of a pair of caudal alae containing most of the vitelline follicles ; with a deep genital atrium provided with a genital sphincter leading into the hermaphroditic pouch, the ventral part of which evaginates to form a large genital papilla ; male and female ducts opening separately to the surface ; vas deferens in the form of a vesicula seminalis separated from the ejaculatory duct by a valve provided with characteristic ciliated cells ; ejaculatory duct lined with ciliated epithelium.

Type and only genus : *Brumptia*, with one species, *bicaudata* (Poirier, 1908), parasitic in the African elephant and rhinoceros, with the characters of the subfamily ; with the lymph system very conspicuously developed ; with testes divided into a large number of small lobes and the ovary subdivided internally ; receptaculum seminis uterinum present.

ACKNOWLEDGMENTS

The author wishes to express her thanks to the Executive Council of the Commonwealth Agricultural Bureaux and to the Director of the Commonwealth Bureau of Helminthology for making it possible for her to spend two months in the Institut de Zoologie, Université de Neuchâtel, to Professor W. Kershaw of the Liverpool School of Tropical Medicine and Mr S. Prudhoe of the British Museum (Natural History) for the loan of material, and to Professor R. T. Leiper for his support and encouragement. She finds it difficult to thank Professor J. G. Baer adequately for his hospitality in the Institut de Zoologie, Université de Neuchâtel, for providing the bulk of the material on which this work is based, and for his practical assistance, friendly criticism and advice ; without him this work could not have been undertaken.

REFERENCES

Fukui, T. (1929). Studies on Japanese amphistomatous parasites, with revision of the group. *Jap. J. Zool.* **2** : 219-351.

MacCallum, G. A. (1917). A new species of trematode (*Cladorchis gigas*) parasitic in elephants. *Bull. Amer. Mus. nat. Hist.* **37** : 865-871.

Maplestone, P. A. (1923). A revision of the Amphistomata of mammals. *Ann. trop. Med. Parasit.* **17** : 113-208.

Näsmark, K. E. (1937). A revision of the family Paramphistomidae. *Zool. Bidr. Uppsala* **16** : 301-565.

Poirier, J. (1909) Trématodes parasites de l'éléphant d'Afrique. *C. R. Ass. franç. Av. Sci.* 37th session, 580-581.

Skryabin, K. I. (1949). [Revision of the systematics of the trematode Order Paramphistomata Skryabin & Schulz, 1937.] *C. R. Acad. Sci. U.R.S.S.* **65** : 919-921. [In Russian.]

Stunkard, H. W. (1925). The present status of the amphistome problem. *Parasitology* **17** : 137-148.

Stunkard, H. W. (1926). On the specific identity of *Amphistomum bicaudatum* Poirier and *Cladorchis gigas* MacCallum. *Anat. Rec.* **34** : 165-166.

Stunkard, H. W. (1929). The parasitic worms collected by the American Museum of Natural History Expedition to the Belgian Congo, 1909-1914. *Bull. Amer. Mus. nat. Hist.* **58** : 233-289.

Travassos, L. (1921). Contribuição para a systematica dos Paramphistodae com uma nota sobre o emprego do phenol em helmintologia. *Brazil-med.* Year 35 **1** : 357-358. [Reprint].

Travassos, L. (1934). Synopse dos Paramphistomoidea. *Mem. Inst. Osw. Cruz* **29** : 19-178.

KEY TO LETTERING OF TEXT FIGURES

B — thickened body wall
C — cuticula of body wall
Cc — layer of cells which secrete cuticula
CC — columnar ciliated cells
ce — ciliated epithelium
cg — cuticula which forms external wall of genital papilla
CM — circular muscles
Cp — cells with ciliated processes
ed — ejaculatory duct
ga — genital atrium
gs — genital sphincter
J — junction of vesicula seminalis and valve

L — lymph canals in hermaphroditic pouch and genital papilla
l — lymph canals in ejaculatory duct
LM — longitudinal muscle
LO — lymph canals in ovary
m — myoblasts
OM — oblique muscle
p — pharyngeal diverticulum
R — receptaculum seminis uterinum
S — sphincter of valve
s — spermatogonia, spermatocytes, spermatozoa, etc.
t — testes
u — uterus
ve — vas efferens
vs — vesicula seminalis
w — wall of hermaphroditic pouch

A REVISION OF THE GENUS *SACCOGLOSSUS* (ENTEROPNEUSTA) IN BRITISH WATERS

BY

C. BURDON-JONES AND A. M. PATIL

Marine Biology Station, University College of North Wales

[Communicated by Professor F. W. Rogers Brambell F.R.S.]

[Accepted 9th February 1960]

(With 3 figures in the text)

A comparative study of topotypes of *Saccoglossus ruber* (Tattersall) *S. serpentinus* (Assheton) and *S. cambrensis* Brambell & Cole shows that they are conspecific, and ought henceforth all to be designated *S. ruber* (Tattersall).

The following characteristics distinguish *S. ruber* from all other species of the genus :— 4 to 6 concentric rings of longitudinal fibres in the proboscis, one proboscis pore on left of stalk, proboscis 3 to 7 times the length of the collar, 45 to 95 pairs of branchial pores, 6 to 12 oesophageal pores—2 to 5 rudimentary, 5 histologically distinct regions in the collar and 3 in the oesophagus.

Munsell, Ridgway and I.S.C.C.—N.S.B. colour designations for the various regions of the body have been tabulated.

CONTENTS

	Page
Introduction	635
Environment	636
Specific characters	638
External morphology	638
Coloration	640
Anatomy	640
Proboscis	640
Collar	642
Trunk	643
Conclusions	643
Comparison with other European species	643
Summary	644
Acknowledgments	644
References	645

INTRODUCTION

The literature records four species of the genus *Saccoglossus* in British waters, viz.,

S. ruber (Tattersall)—west coast of Ireland.

S. serpentinus (Assheton)—west coast of Scotland.

S. cambrensis Brambell & Cole—Welsh coast.

S. horsti Brambell & Goodhart—Solent.

A fifth species, *S. kowalevskyi* (A. Agassiz) has been recorded from Whitstable (Newell, 1949), but this has since been shown to be *S. horsti* (Burdon-Jones, 1950).

In their account of a new enteropneust from Wales, Brambell & Cole (1939) referred to the incomplete nature of the description available for *S. ruber* (Tattersall, 1905) and *S. serpentinus* (Assheton, 1908) and provisionally concluded that *S. cambrensis* was a distinct species, but closely related to *S. ruber*. Since then numerous specimens of *Saccoglossus* have been collected from widely separated localities as well as those from which the holotypes of *S. ruber* and *S. serpentinus* originated. These topotypes bore a remarkable resemblance to *S. cambrensis* and it was suggested (Burdon-Jones, 1950) that on further investigation they might all prove to be the same species.

This account is confined to an examination of the validity of the first three species noted above and shows that *S. serpentinus* and *S. ruber* are probably homeotypic with *S. cambrensis* so that at the present time only two valid species of *Saccoglossus*, viz., *S. ruber* and *S. horsti*, are known from British waters. The distribution of all the enteropneusts known to occur in the British Isles is shown in Fig. 1.

ENVIRONMENT

A comparison of the various littoral habitats from which the topo- and holotypes were collected showed a marked preference for a substrate of clean coarse to fine sand containing variable but small proportions of clay, silt, organic carbon and shell debris (see Table 1). In nearly all instances the substrate was saturated at low water, the water table lying above or immediately below the surface. The Irish topotypes were found in the type locality and areas adjacent to a large bed of *Zostera marina*. The Scottish topotypes were found in greatest numbers on a shore adjacent to that from whence they were originally described and where the marginal vegetation was being eroded and washed down on to the shore. A few comparatively large specimens were found in the type locality. As was noted for *S. horsti* (Burdon-Jones, 1951) and *Protoglossus koehleri* (Burdon-Jones, 1956) the population density diminished rapidly in areas where the drainage was excessive. A coarse to fine underly-

TABLE 1

A comparative analysis of air-dry samples from each of the localities where the holotypes were found.

Species	*S. cambrensis*			
	(Welsh)*		(Irish)	Scottish)
Locality	Black Rocks	Llanddwyn	Ballynakill	Sound of Mull
Sand				
Coarse sand (2·0—0·2)	79·7	11·5	7·9	16·1
Fine sand (0·2—0·02)	11·9	80·8	63·7	66·3
Silt (0·02—0·002)	1·75	0·75	1·97	3·75
Clay (less than 0·002)	3·1	3·9	Trace	7·9
Moisture in the sample	0·2	0·2	0·38	0·8
Calcium carbonate	6·7	4·2	8·74	1·34
Organic carbon	0·108	0·112	0·570	0·810
Nitrogen	0·02	0·02	0·02	—

*After Brambell and Cole (1939).

Fig. 1.—Distribution of the enteropneusta throughout the British Isles and English Channel.

● *Saccoglossus ruber* (Tattersall)

▲ *S. horsti* Brambell & Cole

○ *Protoglossus koehleri* (Caullery & Mesnil) (Southward, 1953)

◑ *Glossobalanus sarniensis* Köehler

△ *Stereobalanus* sp. (Burdon-Jones & McIntyre, 1960)

□ *Glossobalanus marginatus* Meek

1. Sound of Mull ; 2. Clyde (Ettrick and Kames Bay) ; 3. Menai Straits ; 4. Rhoscolyn and Llanddwyn Island ; 5. Nevin ; 6. Ballynakill Harbour ; 7. Dale Fort ; 8. St. Aubin ; 9. Scilly Isles ; 10. Poole Harbour ; 11. Cap de la Hague ; 12. Solent ; 13. Whitstable ; 14. Cap Gris Nez ; 15. Holy Island (Beddmanach Bay) ; 16. Calf of Man ; 17. Port Rush ; 18. Kenmare River ; 19. Scilly Isles ; 20. Eddystone ; 21. Salcombe ; 22. Herme ; 23. Loch Spelve (Mull) ; 24. Glenmore Bay (Loch Sunart) ; 25. Loch Erisort (Lewis) ; 26. Loch Glendhu (Sutherland) ; 27. Farne Islands (Northumberland).

ing gravel substrate was a general, but not invariable, feature of the habitats examined. All were found in irregularly coiled U-shaped burrows, and produced characteristic spiral casts. The burrows frequently had two and occasionally three entrance holes within a radius of some 15 cm. from the spirally coiled cast (Fig. 2).

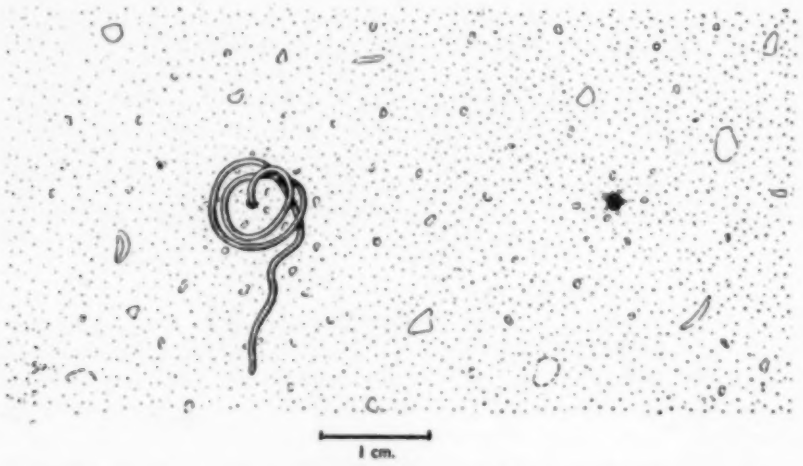


Fig. 2.—Coiled cast and entrance hole to the burrow of *Saccoglossus ruber* (Tattersall).

In the areas investigated the population density attained its maximum within the tidal levels of mean low water neaps to mean low water springs. Off-shore, specimens have been found in muddy sand or mud from depths of 6·2 to 20·0 fm. (Elmhirst, 1934 ; Pike, 1950, 1951).

The associated fauna was fairly typical of sheltered sandy shores. The following species have been recorded. *Acronida brachiata* (Montagu), *Ammodytes tobianus* L., *Arenicola marina* L., *Armandia polyophthalmia* (Kükenthal), *Echinocardium cordatum* (Pennant), *Ensis ensis* (L.), *Eulalia sanguinea* Oersted, *Nephthys caeca* (O.F.M), *Nichomache maculata* (Ardwisson), *Orbinia latreilli* (A. & M.-E), *Sigalion mathildae* A. & M.-E., *Leptosynapta inhaerens* (O.F.M.), *Thracia papyracea* (Poli), *Thyasira flexuosa* (Montagu), *Venus striatula* da Costa, *V. verrucosa* L.

SPECIFIC CHARACTERS

External morphology

Brambell & Cole (1939) distinguished the Scottish form from the other two by its proportionately long proboscis. Though our Scottish specimens were relatively larger in size, the proboscis in both the Welsh and Scottish forms examined had a maximum length of 50 mm. In all the British species of *Saccoglossus*, the collar was longer than broad and thus differed from the continental species, viz.: *S. pygmaeus* (Hinr. & Jac.) in which it is broader than long,

and *S. kowalevskyi* (A. Agassiz) in which length and breadth are equal. The proportion of proboscis to collar was slightly variable in all the three forms, but more so in the Irish specimens (see Table 2.).

TABLE 2

Variations in sizes of mature specimens of the three forms. Measurements made on live specimens.

Species	Total length	Average breadth	Length of the contracted proboscis	Average length of collar	Proportions of proboscis to collar
S. cambrensis	75-150mm.	1·5-2·25 mm.	15-18 mm.	3 mm.	5-6 times
Irish topotype	150 mm.	1·7-3·0 mm.	4-14 mm.	2·5 mm.	3-6 times
Scottish topotype	100-200mm.	2·0-3·5 mm.	20-35 mm.	4·5 mm.	5-7 times

TABLE 3

Variation in numbers of oesophageal pores in the three types.

Species	Number of oesophageal pores	Number of rudimentary pores
S. cambrensis	6 to 12	3 to 5
Irish topotype	6 to 10	2
Scottish topotype ..	6 to 9	2

The median dorsal groove of the proboscis, which according to Tattersall (1905) extended only one-third the length of the proboscis in the Irish holotype, extended almost the entire length of the proboscides in all the three forms. The Irish species was further distinguished by its possession of two proboscis pores, but this characteristic has proved unreliable. In none of the specimens examined by Assheton (1908), Brambell & Cole (1939) and the authors was there more than one pore, and that was on the left side of the proboscis stalk.

The operculum of the collar was generally absent. The mid-dorsal longitudinal groove in the posterior region of the collar, hitherto described only in the Scottish species, occurred in several specimens of *S. cambrensis* and some Irish topotypes. Therefore it is of doubtful systematic value.

The number of branchial pores varied considerably in different specimens of the same species. The number varied from 60 to 95 in *S. cambrensis*, from 56 to 66 in the Scottish topotype and from 56 to 64 in the Irish topotype. In juvenile *S. cambrensis* with well developed but immature genital sacs, and of length varying from 5 to 8 cm., the number of branchial pores varied from 28 to 45 pairs. Some juvenile specimens of the Irish topotype had only 45 pairs of branchial pores.

The distribution of the gonads and the development of the gential ridges in the Irish and Scottish topotypes conformed with those described for *S. cambrensis*.

Coloration

The colour of the proboscis varied considerably in different specimens, but the description given for *S. cambrensis* is equally applicable to the others. Its coloration varied from deep strawberry pink for well-coloured specimens in all localities, to a very pale slightly orange tinted pink in some of the Welsh and Scottish specimens. The stalk had a rich rufous-brown coloration in all specimens.

The use of popular names of colours by authors has proved misleading. In an attempt to overcome this, Brambell and Cole have defined more precisely the coloration of *S. cambrensis* by direct comparison with a standard colour chart (Ridgway, 1912). Table 4 gives the more recent Munsell (1947) and ISCC-NSB (Kelly & Judd, 1955) designations for these colours for comparison with other species. It was found that the coloration of the Scottish and Irish topotypes conformed well with this more accurate description.

Anatomy

Proboscis

The nerve layer below the dorso-median groove of the proboscis was of comparable thickness in both the Scottish and Irish topotypes to that of *S. cambrensis*.

The circular musculature of the proboscis was slightly thinner than the adjacent nerve-fibre layer in the three species. The concentric arrangement of the longitudinal fibres is a distinctive specific feature of the genus *Saccoglossus* and in *S. horsti* there are nine or more rings. In *S. cambrensis* there are four to six. This arrangement was said to be completely absent in both the Irish and the Scottish holotypes. Horst (1939) mentioned that the concentric arrangement of the longitudinal musculature was poorly developed in the Scottish species. Both the Irish and the Scottish topotypes examined had four to six clearly defined rings as in the Welsh specimens.

Tattersall described the proboscis cavity as extremely large in the Irish species and Assheton found it to be very small in the Scottish species. In both the topotypes it was found to be very similar to that described for *S. cambrensis* in being narrow in the middle and slightly expanded at the tip. The ventral septum of the proboscis coelom was very short in them all.

The continuation of the left proboscis coelom into a wide median end-sac was also present in all the forms. This end-sac terminated in a blind diverticulum beyond the proboscis pore.

The S-shaped bend of the stomochord anterior to the proboscis skeleton was also a characteristic feature of the Welsh species. A similar bend of the stomochord was observed in the topotypes. Furthermore, the structure of the epidermis of the proboscis, the lateral extensions of the glomerulus, the shape and size of the pericardium were also identical. The pericardium of the Irish species was not large as described by Tattersall (1905), but proportionately of the same size as that of *S. cambrensis*.

In all the three topotypes the proboscis skeleton was found to be similar in shape and size, the end-plate being saddle-shaped (Fig. 3). The skeletons in

TABLE 4

Ridgway, Munsell and ISCC-NBS names and designations for colours of a living specimen of *S. ruber*.

Region	Name of colour (1)	Ridgway colour	Munsell notation	ISCC-NBS designation and key number (2)
Proboscis				
Bright examples	Strawberry pink	5·00-R., d, Pl. I	7·5R 6·4/10·0	m.r0 37
Typical examples	Grenadine to Grenadine pink	7·R-O., b to d, Pl. II	9R 6·0/12·0 to 9R 7·0/10·0	s.r0 35, s.yPk 26
Pale examples	Bittersweet pink	9·OR-O., d, Pl. II	2·5YP 7·0/8·5	m.0 53
Stalk	Vinaceous rufous	7′·R-O., i, Pl. XIV	10R 4·5/9·0	d.r0 38
Collar	Brazil red to Morocco red	5·00-R., i to k, Pl. I	7·5R 4·0/10·5 to 7·5R 3·4/6·0	d.r0 38 to m.rBr 43
Trunk				
Laterally immediately behind collar	Brazil red to Morocco red	5·00-R., i to k, Pl. I	7·5R 4·0/10·5 to 7·5R 3·4/6·0	d.r0 38, m. rBr 43
Branchial region antero-lateral	Ochraceous-tawny	15′Y-O., i, Pl. XV	8·5YR 5·5/7·0	d.OY 72, s.yBr 74
„ „ „ dorsal	Cinnamon brown to Prout's brown	15′Y-O., k to m, Pl XV	7·5YR 3·8/4·0 to 7·5 YR 3·5/3·0	m.Br 58
Genital region—male	Apricot orange	11′. Orange, Pl.XIV	2·5YR 6·0/9·0	m.0 53
„ „ female	Citrine drab	21′. "O-YY. i, Pl. XL	5Y 5·3/4·0	l.01 106
Intestinal region antero-posteriorly	Yellow ochre	17′. O-Y., Pl. XV	10 YR 5·8/7·0	d.OY 72
	through antimony yellow	17′. O-Y., b, Pl. XV	1YR 7·4/7·5	m.OY 71
	to warm buff	17′. O-Y., d, Pl. XV	1Y 7·8/6·0	m.OY 71, p.OY 73, M. Y 87
Red spots	Carmine	1. Red, i, Pl. I	5R 3·4/12·5	v.R 11
Opaque spots	Light buff	17 O-Y., f, Pl. XV	1Y 8·5/4·5	p.OY 73, p.Y 89

(1) After Brambell & Cole, 1939.

(2) The key number refers to the colour synonyms and near synonyms of the ISCC designation.

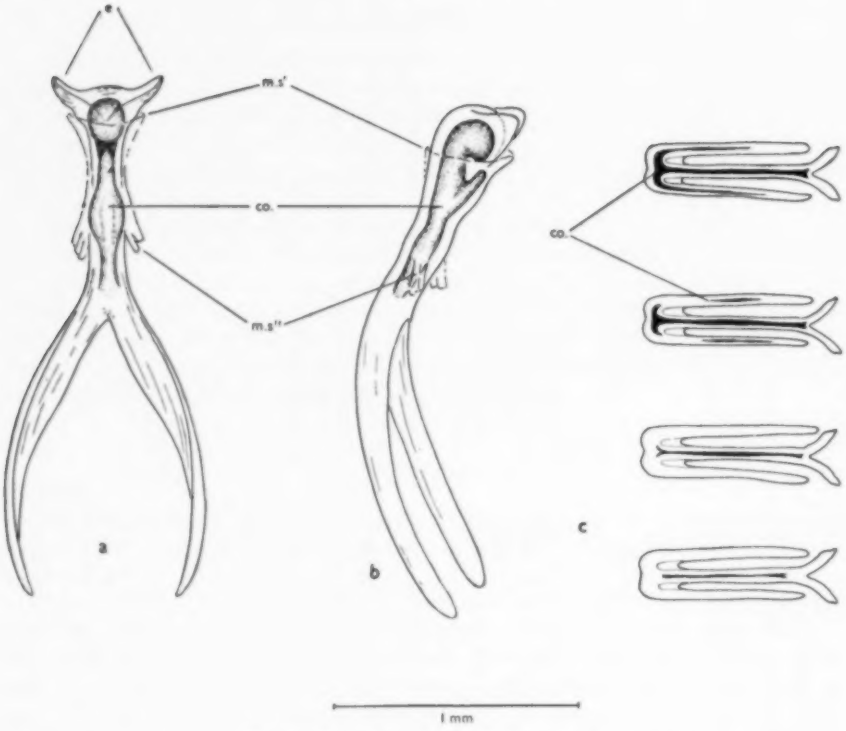


Fig. 3.—Succoglossus ruber (Tattersall)

a. Proboscis skeleton with concretion in stalk, end plates, and ventral hook or keel. Ventral view.

b. Same in lateral view.

c. Selected branchial skeletons showing varying degrees of concretion in the septa and tongues.

co. concretion; e. wings of end-plate ; m.s^{I} insertion of proboscis muscles ; m.s^{II} insertion of collar muscles.

some of the Scottish topotypes and many of *S. cambrensis* showed a prolongation of the ventral keel of the stalk into a hook-like diverticulum near the end-plate. The Scottish and the Irish topotypes showed comparatively less pronounced concretions than those in the skeletons of *S. cambrensis*. In the Scottish specimens examined, concretions were observed only in the basal region of the stalk of the skeleton. Such concretions may be the outcome of age, as there seemed to be a tendency for it to be more prevalent in those forms with the maximal number of branchial pores (see p. 643).

Collar

Five distinct epidermal zones, slightly variable in their relative sizes, occurred in the collar of all the three types. This variation was probably due to the degree of contraction of the collar during fixation. The collar cavities were distinct and the anterior extension of the right cavity varied slightly

in its length in the three types, that of the Irish topotype being longer in proportion than the others. The Scottish and the Irish topotypes resembled *S. cambrensis* in the histological details of the collar-pores, in the presence of two perihaemal cavities, absence of peripharyngeal cavities, anterior deflection of the collar-trunk-septum, the neural keel and its relation to the dorsal nerve cord, the presence of the anterior neuropore and in the absence of the dorsal pouch of the buccal cavity.

Trunk

The mid-dorsal and the mid-ventral grooves, characteristic of the intestinal region of *S. cambrensis*, were also observed in the branchial and hepatic regions of the trunk in the other two topotypes. The structure, shape and arrangement of the branchial skeleton was also the same. In some large specimens of *S. cambrensis* as many as two-thirds of the branchial skeletons in the anterior region had concretions in their septa, and at least one-third had concretions even in the tongues (see Fig. 3). These latter concretions have not hitherto been noticed in the Welsh specimens. Similar concretions were observed in the first few pairs of branchial skeletons of the Scottish topotype but not in the Irish topotype. The epi-branchial ridge was similar to that described in *S. cambrensis*, but in some specimens it was slightly rounded instead of being triangular. Brambell & Cole (1939) have pointed out that the tongues and the septa of the branchial region were of the same width in the Irish topotype. In the Scottish and Irish specimens examined, however, the tongues were found to be either square or rectangular in cross-section, and definitely broader than the septa as in *S. cambrensis*.

In all forms the ventral mesentery was absent in the anterior third of the branchial region. Three histologically distinct regions were distinguishable in the oesophagus. The number of oesophageal pores was variable (see Table 3). The gonads were simple unlobed ovate sacs in both the sexes.

CONCLUSIONS

The description given by Brambell & Cole for *S. cambrensis* is equally applicable to the Scottish and Irish topotypes, except for one feature, viz., the number of branchial pores, which is so variable as to be unreliable when considered apart from other specific characters. We conclude that *Saccoglossus ruber* (Tattersall) and *S. serpentinus* (Assheton) are homeotypes of *S. cambrensis* (Brambell & Cole), and are conspecific with it. In accordance with the rules of nomenclature all these species ought now to be regarded as *S. ruber*. The description of *S. ruber* (Tattersall, 1905) and *S. serpentinus* (Assheton, 1908) are no longer of any systematic value, but the description of *S. cambrensis* by Brambell & Cole (1939), along with the addenda given herein, will prove adequate for the identification of the species.

COMPARISON WITH OTHER EUROPEAN SPECIES

The characteristics of the other species found in British and neighbouring seas in which they differ from *S. ruber* are :—

S. horsti, Brambell & Goodhart (1941), from south coast of England ; large size and the absence of carmine spots on the trunk ; presence of two distinct

grooves extending the whole length of the proboscis ; longitudinal musculature of proboscis in nine or more concentric rings ; presence of a straight stomochord; absence of concretions in the proboscis skeleton ; absence of any longitudinal mid-dorsal groove on the posterior part of the collar ; only four epidermal zones in the collar ; continuity of the neural keel with the tissue of the nerve layer at regular intervals ; trunk lobed in cross-section ; presence of ventro-lateral grooves in the trunk ; 100-140 pairs of branchial pores ; four to eight pairs of oesophageal pores with none rudimentary ; epibranchial ridge bilobed in cross-section ; extreme anterior extension of the gonads.

S. pygmaeus Hinricks & Jacobi (1938) from Helgoland : Extremely small size and absence of any distinct grooves on the proboscis ; absence of concentric arrangement of the longitudinal muscles of the proboscis ; straight stomochord with a slightly developed ventral diverticulum ; broad end-plate of the proboscis skeleton ; posterior margin of the collar forming an operculum ; absence of any longitudinal mid-dorsal groove on the posterior part of the collar; no epidermal zones in the collar ; presence of peripharyngeal cavities ; absence of neural keel ; 9-22 pairs of branchial pores ; only one pair of oesophageal pores; a fairly broad epibranchial ridge ; oesophagus short, uniform and undivided ; gonads begin from posterior end of branchial region.

SUMMARY

1. Comparative characters of *S. cambrensis* and topotypes of *S. ruber* and *S. serpentinus* have been discussed in detail and it is concluded that the three are conspecific and ought henceforth to be designated *S. ruber* (Tattersall).

2. The following are the changes or additions to the specific characters of *S. cambrensis* as given by Brambell & Cole (1939) :—

> Number of branchial pores, 45-95 pairs ; presence of a short longitudinal mid-dorsal groove on the posterior part of the collar ; epibranchial ridge triangular or rounded ; 6-12 oesophageal pores with the first 2-5 rudimentary.

3. *S. ruber* has been compared with the other species of *Saccoglossus* found in the British waters and the neighbouring seas.

ACKNOWLEDGMENTS

We are greatly indebted to Professor F. W. Rogers Brambell, F.R.S., for his advice and criticism of this work and for access to his collection of *S. cambrensis* slides, to Professor P. W. Richards for his kindness in providing laboratory facilities in the Botany Department where part of this investigation was carried out, to Dr M. Abercrombie, F.R.S., Department of Anatomy, University College of London, for the loan of Assheton's original sections of *S. serpentinus*, and to the staff of the Department of Agricultural Chemistry, University College of North Wales, for the analyses of the substrates given on p. 636. We are grateful to the Colombo Plan Organisation and the Browne Research Fund for providing the funds which have enabled the authors to carry out this investigation.

REFERENCES

Assheton, R. (1908). A new species of *Dolichoglossus*. *Zool. Anz.* **33** : 517-20.

Brambell, F. W. Rogers & Cole, H. A. (1939). *Saccoglossus cambrensis* sp. n., an enteropneust occurring in Wales, *Proc. zool. Soc. Lond.* (B) **109** : 211-36.

Brambell, F. W. Rogers & Goodhart, C. B., (1941). *Saccoglossus horsti* sp. n., an enteropneust occurring in the Solent. *J. Mar. biol. Ass. U.K.* **25** : 283-301.

Burdon-Jones, C., (1950). Records of British enteropneusta. *Nature, Lond.* **165** : 636.

Burdon-Jones, C., (1951). Observations on the spawning behaviour of *Saccoglossus horsti* Brambell & Goodhart, and of other enteropneusta. *J. Mar. biol. Ass. U.K.* **29** : 625-38.

Burdon-Jones, C. (1956). Observations on the enteropneust *Protoglossus kochleri* (Caullery & Mesnil). *Proc. zool. Soc. Lond.* **127** : 35-58.

Burdon-Jones, C. & McIntyre, A. D. (1960). *Stereobalanus*, a genus new to the Old World. *Nature, Lond.* **186** : 491-2

Elmhirst, R. (1934). Enteropneusts in the Clyde Sea-Area. *Nature, Lond.* **134** : 183.

Horst, C. J. Van der (1939). Hemichordata. *Bronn's Klassen u. Ordn. d. Tierreichs* **4** : Abt. 4, Buch 2, Tiel 2.

Jacobi, L. (1941). Morphologie und Anatomie des Enteropneusten *Saccoglossus pygmaeus*, Hinr. & Jac. *Helgoland Wissen. Meeresunters.* **2** : 163-182.

Kelly, K. L. & Judd, D. B. (1955). The ISCC—NBS method of designating colors and a dictionary of color names. *National Bureau of Standards*, Circular 553, Washington, D.C.

Newell, G. E. (1949). Occurrence of *Saccoglossus kowalevskyi* (?) on the North Kent coast. *Nature, Lond.* **164** : 747.

Pike, R. (1950-51). Personal communications.

Purchon, R. D. & Jefferson, G. T. (1949). A hemichordate from West Wales. *Nature, Lond.* **164** : 881.

Ridgway, R., (1912). *Color standards and color nomenclature*. Washington.

Southward, E. (1953). Personal communication.

Tattersall, W. M. (1905). Enteropneusta from west coast of Ireland. *Ann. Rep. Fish., Ireland, Sci. Invest.* 1902-3 : 213-214.

STUDIES OF THE HANDS OF LIVING PRIMATES

BY

J. R. NAPIER

Royal Free Hospital School of Medicine, London.

[Accepted 9th February, 1960]

(With 3 plates and 3 figures in the text)

A study of passive movements and an analysis of the prehensile patterns of movement of the anthropoid ape hand was carried out in two young chimpanzees and one young orang-utan, all approximately two years old at the time of study. The passive movements compare closely with those of a human child except in respect of the wrist and metacarpo-phalangeal joints of the fingers ; in the case of the former joint, while flexion was very full, extension was limited. Passive movement of the metacarpo-phalangeal joints was also very full, movement being limited only by contact of the fingers with the palm. A " double-locking " mechanism of the 2-5th digits taking place at the metacarpo-phalangeal joints is described. The anatomical basis of these movements and the " double-locking " mechanism is discussed. Active movements were studied in terms of the prehensile patterns of the human hand (Napier, 1956) and it is shown that, while there is evidence of a functional duality of prehension in the hands of young anthropoid apes, the execution of the two grips differs profoundly from that of Man ; the difference is discussed in terms of the disproportion in the length of the thumb and fingers in apes. It is suggested that the " double-locking " mechanism of the fingers compensates in some measure for the ineffectiveness of the thumb in prehension.

CONTENTS

	Page
Introduction	647
General appearance	649
Passive movements	649
Anatomical considerations	651
Active movements	652
Discussion	653
Acknowledgments	656
Summary	656
References	656

INTRODUCTION

In a previous paper (Napier, 1956) a method of analysing the prehensile movements of the hand was presented. Prehensile movements are defined as those by which an object, whether fixed or free, is seized and held, partly or wholly, within the compass of the hand. Non-prehensile movements, on the other hand, are those in which no grasping or seizing is involved, but by which objects can be manipulated by pushing or lifting motions of the hand as a whole or the digits individually. Prehensile movements, in turn, may be further analysed into two functional patterns or complexes that are termed *precision grip* and *power grip* (Pl. 1, fig. 1 a & b). It appears that these two grips embody the whole range of prehensile activity of the human hand, for it is a matter of observation that if the hand is arrested during the performance of prehension it inevitably exhibits a phase of one or other of the two grips.

The precision grip is employed where delicacy and precision of movement are required ; the application of muscular power being a secondary consideration. In contrast, the dominant characteristic of the power grip is the application of force ; delicacy and precision being of secondary importance. Anatomically the two functions of the hand in Man may be defined thus :—

Precision Grip. The object is gripped between the palmar aspect of the terminal phalanx of the finger or fingers and the thumb.

Power Grip. The object is held as in a clamp between the flexed fingers and the palm, counter pressure being applied by the adducted thumb.

The present communication, which is the first of a series of studies of the movements of the hands of living Primates, was carried out with this concept of functional duality in mind. In view of the generalized nature of the Primate hand, phylogenetically speaking, it seemed probable that in spite of the extreme locomotor adaptations of these forms similar patterns of prehension would be apparent in the hands of anthropoid apes.

The use of the terms precision and power grip in Man is based on a premise, confirmed by observation, that it is the purpose to which the grip is to be put rather than the size or shape of the object that, in the first instance, governs the posture adopted by the hand. There is a degree of purposiveness implicit in these terms that it would be improper to attribute to anthropoid apes without further knowledge of the part played by imitative action on the one hand, and the so-called " behaviour with insight " (Yerkes & Yerkes, 1929) on the other.

As Hayes & Hayes have pointed out (1954), there is an inherent difficulty in transposing concepts, that have their source in the behaviour of humans, into terms of " non-cultural, non-linguistic and uneducated subjects". This difficulty is avoided here by omitting any reference to " purpose " and confining the observations to matters of behaviour, structure and form, with this in mind it might be considered necessary that the terms employed to describe the two grips in anthropoid apes should relate only to posture ; this however, would involve the introduction of a new terminology which, on general principles, is thought inadvisable. Thus in transposing the concepts of power and precision grip from Man to anthropoid apes the author wishes to emphasise his awareness of the difficulty and to stress that in spite of the subjective nature of the terms used, their definition is purely anatomical and does not imply any element of purposiveness.

Wooden cylinders and rubber balls of various diameters are the most useful standardized test objects in analyzing function of the human hand. In carrying out tests with chimpanzees and orangs the " cylinders " used were sticks or broom handles and the " spheres ", grapes or sugar coated sweets. These are objects which lie within what Kohler (1925) refers to as the *range of function* of apes.

The following observations were made over a period of six months on the hands of two young chimpanzees (" Penny " and " Suki ") and one young orang (" Alex "), then residing in the Chimpanzee Nursery in the Zoological Gardens in London. The two chimpanzees were two years old at the beginning of the study and the orang was approximately the same age. All three

animals were extremely co-operative and it was possible to carry out a full examination of active and passive movements.

GENERAL APPEARANCE

The general appearance of the hands of chimpanzees and orangs is too well known to merit lengthy description. There are certain features, however, that are relevant to the present considerations. The thumb in both genera is short, conical and somewhat degenerate looking ; it falls short of the base of the free index finger in *Pan* and barely reaches the second metacarpo-phalangeal joint in *Pongo* (Midlo, 1934). The fingers are long and relatively slender in both genera, having nevertheless a somewhat bulbous appearance in the proximal segments. The finger tips are cone-shaped—markedly so in *Pongo*—and differ profoundly from the broad spatulate pulps of Man. The thenar and hypothenar eminences are small and flat and have the appearance of half empty bags of skin. There is no backward projection or " heel " to the hand that is so prominent a feature of the hand in lower Primates. The flexion folds of the palm are in two series—transverse and longitudinal. The oblique lines of the human palm are entirely absent.

Finally mention should be made of the " position of rest ". This is a functional concept originally described by Ellis (1878) and describes the position taken up by the part at rest under the normal postural tone of the muscles acting on the part. The " position of rest " of the human hand which is subject to considerable individual variation has been well described and illustrated by Wood Jones (1941). The posture reflects the functional potentialities of the hand which lies in a position intermediate between that of a power grip and that of the precision grip (Pl. 1, fig. 1). The ape hand at rest (Fig. 2), while in marked contrast to the human condition (Fig. 1), reflects in a similar manner its own particular patterns of prehensile movement.

PASSIVE MOVEMENTS

The range of passive movements in the hands of the three young anthropoid apes was comparable to that found in Man of equivalent age in respect of all joints except the wrist and the metacarpo-phalangeal joints of the thumb and fingers. The findings with reference to these joints are summarized in Table 1.

Wrist joint : At the wrist the most striking feature was the large flexion and small extension range. In the chimpanzee flexion was through approximately 140° and in the orang-utan was slightly less. Extension did not exceed 30° in either genus while the fingers were maintained in extension but reached approximately 60° when allowed to flex. The ulnar deviation of the wrist in both genera was less than in Man while radial deviation is equally limited in both Man and anthropoid apes.

Thumb joints : The thumb of the three young apes was extremely mobile and could be passively hyperextended until it reached a plane nearly parallel to that of the forearm. Much of this mobility was occuring at the metacarpo-phalangeal joint of the thumb which could be freely flexed, extended, abducted and adducted and, in addition, axially rotated through 30°. The range of

Fig. 1.—The posture of the human hand at rest drawn from life. The subject is an adult male. Note the differential curling of the fingers and the posture of the thumb intermediate between abduction and adduction.

Fig. 2.—The posture of the anthropoid ape hand at rest. The subject is an adult female chimpanzee. Note the slight hooking of the fingers at the proximal interphalangeal joint and the adducted thumb.

movement in all directions but particularly in abduction was considerably greater in the orang than in the two chimpanzees. While abduction, adduction and rotation also occurs at this joint in Man as well as flexion and extension (Napier, 1952) the range is considerably greater in anthropoid apes.

In spite of a discrepancy in length between the index finger and thumb, the two digits in both genera could be placed in opposition by acutely flexing the index finger at its interphalangeal joints and widely abducting the thumb. The movement of opposition as it is understood in Man,* (Pl. 1, fig. 2) however, is never performed actively by either genus and therefore the flexibility that permits it is a measure of mobility of the hand rather than a pointer to function.

**Opposition*. A movement of the thumb as a whole in which the pulp surface is placed squarely in contact with, or diametrically opposite to, the pulp surface of one or all of the remaining digits.

TABLE 1

Comparison between the ranges of certain movements of the joints of the wrist and hand in which young anthropoid apes differ from the human child.

		Chimpanzee	Orang-utan	Man
Wrist Joint	Flexion	+++	++(+)	++
	Extension (fingers extended)	+	+	+++
	Ulnar deviation	+(+)	+	++
	Radial deviation	+	+	+
Thumb				
C-M joint	All movements	+(+)	++	+++
M-P joint	All movements	++(+)	+++	+
Fingers				
M-P joints	Flexion	+++ (170°)+/−	+++ (170°)+/−	+(+) (90°)+/−
I-P joints	Extension	++(+)	++(+)	+++

+++ = large range ++ = medium range + = small range.

The movements of the carpo-metacarpal joint of the thumb while similar to those of Man are not so full and free.

Joints of the fingers : The most outstanding feature of the finger movements, which otherwise closely correspond to those of Man, was the range of flexion possible at the metacarpo-phalangeal joints. In all three apes the fingers could be flexed passively until further movement was limited by contact with the palm. The range was approximately 170° which is in marked contrast with Man in whom these joints can seldom be flexed actively or passively beyond 90°. The acutely flexed finger tips could be " locked " into the skin fold at the base of the digits and then, by further flexion of the metacarpo-phalangeal joints, could be " double-locked " by rolling the flexed and " locked " digits into the palm (Pl. 1, fig. 3). This locking mechanism is also apparent in the hands of adult chimpanzees and orangs.

ANATOMICAL CONSIDERATIONS

The limited range of wrist extension as several authors (Wilder, 1861 ; Schultz, 1936 ; Straus, 1940) have pointed out is due to a relative shortening of the long flexors of the fingers notably the flexor digitorum profundus. That such is the case is readily apparent in the living chimpanzees and orangs for there is an immediate augmentation of wrist extension on flexing the fingers or flexing the elbow. Straus, (1940) observes that this condition of relative congenital shortening increases post-natally ; thus the dorsiflexion range in the present series of young apes may be expected to decrease with age.

The anatomical basis for the mobility of the metacarpophalangeal joint of the thumb in both apes and, particularly, in the orang lies in the shape of the distal articular surface of the first metacarpal which is well rounded but asymmetrical and somewhat tilted towards the radial side (Napier,1959). The

carpo-metacarpal joint is poorly developed in both chimpanzees and orangs particularly in respect of the anterior-posterior concavity.

The extensive range found at the metacarpo-phalangeal joints of the chimpanzee and orang is related to the observation that the heads of the metacarpals in Ponginae are set at an angle to the shaft, the articular surface being directed anteriorly as well as distally (Napier, 1959); this arrangement permits a much greater degree of finger flexion in anthropoid apes than in Man in whom the articular surface is directed wholly distally.

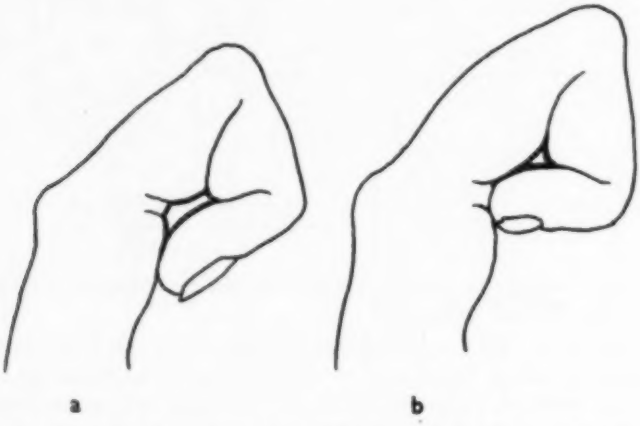


Fig. 3.—The " double-locked " posture of the medius in (a) the human hand, (b) the anthropoid ape hand (orang-utan). Note that a cylindrical object gripped as in (b) would be more completely enclosed than when gripped as in (a).

The curious locking mechanism of the young anthropoid hand appears in chimpanzees to be related to the relatively long proximal segment of the digits. In Man the combined lengths of the middle and distal phalanges are greater than the length of the proximal phalanx. In chimpanzees the proximal phalanx is of equal or greater length than the combined lengths of the middle and distal phalanges. This permits the finger flexed at the proximal interphalangeal joint to tuck into the metacarpo-phalangeal skin-joint at its base thus completely enclosing any slender object so gripped (Fig. 3).

ACTIVE MOVEMENTS

Precision Grip: The acme of precision in Man is the ability to pick up small objects between thumb and index finger and hold them delicately yet securely between the opposed pulp surfaces (Pl. 1, fig. 2). This posture demands perfect opposability of the thumb at the metacarpo-phalangeal joint as well as at the carpo-metacarpal joint. Young anthropoid apes are incapable of assuming this posture owing to the relative shortness of their thumbs. Small objects are picked up from a flat surface by chimpanzees in a number of different ways, among which the following were the most commonly observed :—(1) By means

of the pulp of the thumb and the side of the middle or terminal phalanx of the index finger (Pl. 2, fig. 4) ; (2) By means of the side of the thumb and the side of the middle phalanx (Pl. 2, fig. 5) ; (3) By means of the dorsum of the thumb and the dorsum of the terminal phalanx (Pl. 2, fig. 6). While the two chimpanzees almost invariably used the finger and thumb grip to pick up small objects the orang seldom would do so unless forced by circumstances to adopt this posture. A grape proferred between finger and thumb, for instance, would be grasped in a somewhat unstable manner between the tip of the terminal phalanx of the thumb and some part (usually the side of the proximal phalanx) of the index finger (Pl. 2, fig. 7). Objects proferred on the flat of the hand were most frequently scooped up by the fingers (Pl. 2, fig. 8) although a finger and thumb grip was occasionally used. Small objects picked up from the ground were invariably seized by the fully supinated hand between the adjacent sides of the middle phalanges of the index and middle fingers from whence they were transferred to a palmar grip.

Although the chimpanzees were more precise than the orang in picking up small objects, the inadequacy of their opposition made it difficult for them to perform delicate tasks such as undoing a button. This exercise was carried out bimanually ; two index fingers of the same length being more effective than one finger and a disproportionately short thumb (Pl. 2, fig. 9).

Power Grip : While the thumb at least contributes—though ineffectively—to the precision grip it plays little or no part in the power grip which is produced solely by flexion of the fingers in both chimpanzees and orangs. The grip may be either hook-like when the metacarpo-phalangeal joints are extended and the remaining joints flexed (Pl. 3, fig. 10) or fist-like when all finger joints are flexed (Pl. 3, fig. 11). In the hook-like grip the thumb is too remote to contribute any stability ; in the fist-like grip the thumb rests loosely against the cylinder or is folded into the palm, but in neither posture is it playing an essential part. When the orang is hanging from an overhead branch the thumb is abducted at tight angles to the palm (Pl. 3, fig. 13), taking no part in the grasp.

On occasions when the test object happens to lie obliquely across the palm, the thumb may momentarily bear a human-like relationship to it (Pl. 3, fig. 12) but it is more likely to be tucked away in the palm (Pl. 3, fig. 14).

The great power of finger grip can be demonstrated in both orangs and chimpanzees by means of a thin piece of string or cord. This can be gripped by finger flexion alone and held against a strong direct pull (Pl. 3, fig. 15), a facility that is denied to Man. It seems likely that the ability to grip a piece of string in this fashion is related to the " double-locking " mechanism described above. The tips of the fingers tucking in to the metacarpo-phalangeal joint line serve to enclose the string completely and, thus, to increase the frictional resistance to traction.

DISCUSSION

It must be stressed that this study is concerned only with the structural differences in the hand of anthropoid apes and Man and the effect that these, alone, produce on function. The elaboration of the nervous system which

provides the basis of human manual skill would clearly have to be taken into account were the *performance* of prehensile movements—rather than the physical ability to perform them—in question.

The proportions of the human hand are such that the tips of all five digits can be brought together meeting at a point in space in the line of the axis of the middle finger. At the point of convergence the digits are effectively the same length. No anthropoid ape can achieve this posture owing to the marked disproportion in length of the thumb and fingers. The human thumb at the point of convergence is fully opposed to the remaining digits, thus it can be deduced that since anthropoid apes are incapable of achieving this posture they are *ipso facto* incapable of opposition. Much has been written regarding opposition in Primates and many contrary opinions have been expressed (Hepburn, 1891 ; Hayes & Hayes, 1954 ; Le Gros Clark, 1934). Disagreement, as is so often the case, is largely attributable to a semantic difficulty. The term opposition has no uniform connotation among human anatomists and zoologists and it is not surprising that confusion exists. To a human anatomist opposition has a special meaning and signifies the movement of the thumb as a whole in relation to one of the remaining digits (see footnote p. 650) ; to a zoologist the term has a more general import ; in a static sense it implies that the thumb is set at an angle or even opposite to the remaining digits as in certain birds and reptiles (schizodactyly) or, in a dynamic sense, is capable of being moved to such a position by muscular action, as in most Primates.

Thus, in stating that anthropoid apes can not oppose the thumb, the human anatomist is not denying that the ape is capable of rotating the thumb until it faces the remaining digits, or even of achieving a make-shift type of opposition ; he is merely stating that the pulp-to-pulp contact of thumb and digits that forms the anatomical basis of Man's precision grip is not possible in these forms. To many human anatomists, opposition is a " hallmark of mankind ", to many zoologists, it is simply a function of the Primate hand.

The nearest that the chimpanzee can get to opposition in the human sense is a tenuous and unstable grip between the extreme tip of the thumb and the extreme tip of the acutely flexed finger. This posture is well illustrated in a photograph of the Hayes' home-reared chimpanzee, Vicki, holding a lighted cigarette (1954). Clearly this grip is neither as effective from the point of view of motor or sensory function as it is in Man. This posture was on no occasion duplicated by either chimpanzees under observation in this study ; indeed, it is to be doubted whether a posture so entirely non-functional would ever voluntarily be employed by a chimpanzee.

In young anthropoid apes the thumb plays considerably less part in the power grip than the precision grip. In Man it contributes to the grip in two ways. Firstly in its strongly adducted position it constitutes a buttress on the lateral side of the hand ready to resist forces of traction and leverage acting on the object held ; secondly, it provides, by small adjustments of posture, a means of controlling the precise direction in which a force is being applied. The thumb of young apes is not sufficiently long or strong to contribute to the power of the grip in this manner. The deficiency of the thumb, however, is in some measure compensated for by an increase in the length and strength of the

fingers. The strength and effectiveness of digital flexion is exemplified particularly by the " double-locking " mechanism described above. This mechanism, which does not appear to have been previously recorded, was observed in the hands of all three apes. The " double-locking " action of the fingers which is analagous to the type of lock known to engineers as an over-centre lock, provides extremely powerful resistance to traction and leverage. Although it is not clear why such a mechanism should exist, it apparently serves as a substitute for the thumb in gripping slender branches. The mechanism, possibly, can be correlated with the need to grasp and tug the tender shoots of plants and shrubs while feeding.

The function of the thumb in the human power grip is directly responsible for the obliquity of the axis of the grip. Only when placed obliquely across the palm can a cylindrical object be stabilized by the fingers and at the same time buttressed and controlled by the thumb. The thumb of the chimpanzee and orang is too short to provide an adequate buttress and, since it takes little or no part in the power grip, there is no reason for the grip to be an oblique one ; in fact this posture is seldom employed by anthropoid apes except incidentally; the relative unimportance of this grip to the Ponginae is reflected in the poor development of the hypothenar group of muscles, in the absence of obliquely placed palmar flexion folds and in the attitude of the hand at rest. (Fig. 2).

There is thus evidence in this behavioural study of a functional duality in the hands of young chimpanzees and orangs. Objects may be gripped by flexion of the fingers alone (cf. human power grip) or by the interaction of the fingers and thumb (cf. human precision grip). The fact that the execution of these two grips differs profoundly in Man and apes may be related to differences in the form of the hands particularly in respect of the relative proportion of the thumb and fingers. Schultz (1930) has demonstrated the relative disproportion of the anthropoid ape thumb by expressing its length as a percentage of the middle finger ray length with the following results. *Pan* 39·5 per cent *Pongo* 34·6 per cent *Homo* (white) 64·4 per cent. This disproportion may be regarded as an adaptive change related to the specialized locomotor habits of chimpanzees and orangs. Brachiation in these forms is facilitated by a hand with long digits, which are used in a hook-like manner to grasp the branches during overhead swinging, and a short, feeble but freely mobile thumb that permits a quick and unhampered release from the overhead grip.

Other differences between the human hand and the chimpanzee and orang hand that may be regarded as secondary, include the degenerative condition of the long flexor of the thumb (Straus, 1942 a & b, 1946) and the poorly developed, though quite well differentiated, thenar and hypothenar musculature.

Catarrhine primates, with certain exceptions, possess thumb-finger ratios that are closer to Man's than to those of the three great apes (Schultz, 1930) ; in addition they possess a relatively well developed intrinsic thenar musculature It is interesting to observe that the exceptions mentioned above which include the thumbless Colobus monkey and certain of the short-thumbed langurs, are specialized and habitual arboreal forms that occasionally employ some degree of brachiation as a means of locomotion. This type of locomotion has been referred to elsewhere as *generalized* brachiation in contrast to the specialized

brachiation of, for example, the gibbon (Napier, 1959). The catarrhine primates whose thumb-finger ratios approach closely to Man's include forms, on the other hand, that are either wholly terrestrial (baboons, Patas and Nisnas monkeys), or part terrestrial (macaques and some guenons). The baboons—the most thoroughly terrestrial of all catarrhine primates—have a thumb-finger ratio (Schultz, 1930) second only to Man himself.

Clearly a study of the mechanism of grasp in terrestrial quadrupedal forms would be of value.

ACKNOWLEDGMENTS

My thanks are due to the Zoological Society of London for permission to publish this account. I am also indebted to Dr W. C. Osman Hill for his help and advice ; to Mrs Pinto Leit who, at the time of this investigation, was in charge of the Chimpanzee Nursery and to Mr Laurie Smith, Head Keeper of the Monkey House. Text figures 1 and 2 were the work of Mr Maurice Wilson.

The photographs were taken by Mrs Pat Thomas and Mr J. Crane of the Photographic Department of this School.

I am indebted for the generous financial help to the Endowment Fund of the Royal Free Hospital.

SUMMARY

In a previous paper (Napier, 1956) an analysis of the prehensile movements of the human hand was presented. These movements were classified as *power grip* movements and *precision grip* movements. This same concept of functional duality is employed in the present work for the study of prehensility in two young chimpanzees and a young orang.

The following investigations were carried out :—

(1) The external appearance of the hands with special reference to the palmar flexor lines and the " position of rest ".

(2) The range of passive movements in the joints of the wrist and hand.

(3) Active movements of manual prehension using standardized test objects ; the imperfect function of the thumb during the performance of these activities is especially noted. A mechanism of the pongid hand, apparently previously unrecorded and referred to as "double-locking " is described.

Certain observations are discussed in the light of the brachiating adaptations of the pongid hand.

REFERENCES

Clark, W. E. Le Gros (1934). *Early forerunners of man.* London.

Ellis, T. (1878). The position of rest in fatigue and pain. *Brit. Med. J.* **1** : 84.

Gregory, W. K. (1951). *Evolution emerging.* New York : Macmillan.

Hayes, K. J. & Hayes, C. (1954). The cultural capacity of chimpanzee. *Hum. Biol.* **26** : 288-303.

Hepburn, D. (1891). Integumentary grooves of the palm of the hand and the sole of the foot of man and anthropoid apes. *J. Anat. Phys.* **27** (N.S.7) : 112-130.

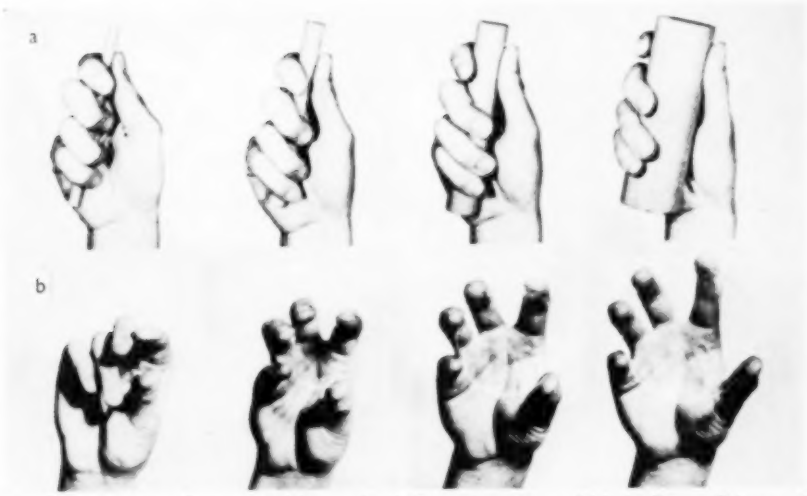


Fig. 1.—Four postures of the normal human hand illustrating phases of (*a*) the Power Grip complex; (*b*) the Precision Grip complex.

Fig. 2.—Human hand with thumb and index finger in opposition.

Fig. 3.—"Double-locking" mechanism demonstrated in the hand of young orang-utan, "Alex."

Fig. 4.—"Penny" picking up a sugar-coated sweet in a precision grip.

Fig. 5.—"Penny" taking a grape in a finger and thumb precision grip.

Fig. 6.—"Penny" taking a grape from the flat hand in a precision grip.

Fig. 7.—"Alex" picking up a grape in a precision grip.

Fig. 8.—"Alex" holding a grape in a curled hand after scooping it up with the fingers.

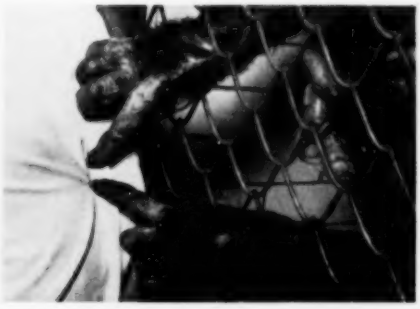


Fig. 9.—"Penny" using right and left index fingers to undo a shirt button.

Fig. 10.—"Alex" holding on to a broom handle by a "hook-like" power grip.

Fig. 11.—"Alex" grasping a stick in a "fist-like" power grip.

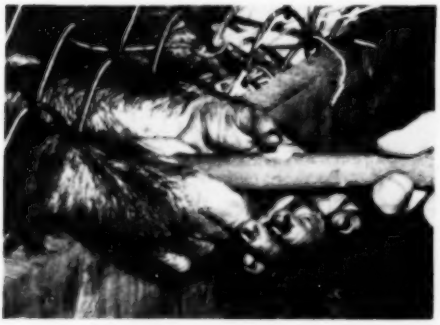


Fig. 12.—"Penny" showing a remarkably human power grip posture.

Fig. 13.—"Alex" suspended from a branch. Note the widely abducted thumb.

Fig. 14.—"Penny" gripping a stick. Note the thumb flexed and adducted into the palm.

Fig. 15.—"Alex" showing the "double-locking" mechanism in action when pulling on a piece of string.

KEITH, H. H. (1924). Racial differences in the papillary lines of the palm. *Amer. J. Phys. Anthrop.* **7** : 165-206.

KOHLER, W. (1925). *The mentality of apes.* English translation by Ella Winter 1957, London. Penguin Books.

MIDLO, C. (1934). The form of the hand and foot in primates. *Amer. J. Phys. Anthrop.* **19** : 337-389.

NAPIER, J. R. (1952). The attachments and function of abductor pollicis brevis. *J. Anat.* **86** : 335-341.

NAPIER, J. R. (1956). The prehensile movements of the human hand. *J. Bone Jt. Surg.* **38B** : 902-913.

NAPIER, J. R. (1959). Fossil metacarpals from Swartkrans. *Fossil mammals of Africa* No. 17. London : British Museum (Natural History).

NAPIER, J. R. (1959). The problem of brachiation among the Primates. *Sitz. B. Deutschen Gesell. Anthrop.* (Auszug.)

SCHULTZ, A. H. (1930). The skeleton of the trunk and limbs of higher primates. *Hum. Biol.* **2** : 303-438.

SCHULTZ, A. H. (1936). Characters common to higher primates and characters specific for man. *Quart. Rev. Biol.* **11** : 259-283 ; 425-455.

STRAUS, W. L. (1940). Posture of the great ape hand in locomotion. *Amer. J. Phys. Anthrop.* **27** : 199-207.

STRAUS, W. L. (1942). The homologies of the forearm flexors : urodeles, lizards and mammals. *Amer. J. Anat.* **70** : 281-316.

STRAUS, W. L. (1942). Rudimentary digits in primates. *Quart. Rev. Biol.* **17** : 228-243.

STRAUS, W. L. (1946). The hand and foot musculature of catarrhine Primates. *Amer. J. Phys. Anthrop.* n.s. **4** : 263 (abstract).

WILDER, B. G. (1861). Contribution to the comparative myology of the chimpanzee. *Boston J. nat. Hist.* **6** : 353-384.

WOOD-JONES, F. (1941). *The hand.* 2nd Edit. London : Baillière, Tindall & Cox.

YERKES, R. M. & YERKES, A. W. (1929). *The great apes.* New Haven : Yale University Press.

EARLY PRONEPHRIC GROWTH IN *NEOCERATODUS* LARVAE

BY

H. FOX

Department of Zoology and Comparative Anatomy,
University College, London

[Accepted 9th February, 1960]

(With 1 plate)

The pronephric systems of eight *Neoceratodus* larvae ranging from 11·5 to 16 mm. total length were analysed quantitatively and the measurements were treated statistically for two groups of mean total length 11·5 mm. and 15·3 mm. In the 15·3 mm. group the means of the measurements of the nuclear population, total volume of cells, overall pronephros volume and the internal surface area of the tubules show a significant superiority over the means of those in the 11·5 mm. group, but the mean of the glomus length is significantly lower. The individual cell volume which does not change significantly had a maximum range of 6500-6800 μ^3. Quantitatively in terms of cell volume and qualitatively the pronephric systems of larvae of *Neoceratodus*, Anura and urodeles are similar, and have evolved in a parallel manner during phylogeny.

CONTENTS

	Page
Introduction	659
Material and methods	659
General description of the *Neoceratodus* larvae	660
The pronephric system	660
Discussion	662
Acknowledgments	662
References	663

INTRODUCTION

There is a vast literature on the structure and development of *Neoceratodus* (see Semon and associates, 1893-1913 ; Greil, 1908, 1913 ; Goodrich, 1930 ; Edgeworth, 1935 ; De Beer, 1937 ; among many others), yet quantitative information about various components of its pronephric system is either rare or non-existent. The following quantitative description of the pronephric systems of a small collection of *Neocratodus* larvae is a contribution to this somewhat neglected field.

MATERIAL AND METHODS

Pronephric components and glomera of eight *Neoceratodus forsteri* ? larvae were measured. The larvae were arbitrarily separated into two groups ; the first group contained three specimens each 11·5 mm. long, and the second group included four specimens : a 14 mm. and a 15 mm. specimen and two each 16 mm. long (mean total length 15·3 mm.). An intermediate specimen 13·5 mm.

long was likewise measured. One further 13·5 mm. larva was sectioned horizontally at 10 microns in order to measure nuclear length, and for 250 nuclei the mean measurement was 11·913 $\pm$ 0·1586. Previous results in Amphibia showed that nuclear length does not significantly change during early development ; it is most unlikely to have occurred in the short period under review, therefore 12 μ was used as the correction factor to reduce the crude nuclear count to an absolute one (Abercrombie, 1946). All specimens blocked in paraffin wax and sectioned transversely at 10 microns were stained with haematoxylin and eosin. Quantitative methods were the same as those used in previous experimental work on urodele larvae (Fox, 1955, 1956, 1957, 1959). The level of significance used throughout was $P < 0{\cdot}05$.

GENERAL DESCRIPTION OF THE *NEOCERATODUS* LARVAE

The 11·5 mm. larva has an open mouth and gill clefts and a well formed opercular fold. Small nasal sacs open into the anterior roof of the mouth. The eyes possess a solid lens. There is no fully developed gut, the oesophagus ends blindly in the yolk mass just behind the pronephros, but the yolk shows signs of vacuolisation—the first indication of gut formation. Chondroblasts have accumulated in the prospective cartilage regions of the head and pharynx and there is some incipient cartilage formation, although true cartilage was shown in the 11·0 mm. stage (Edgeworth, figs. 15, 19, 20, 1935). Blastemata of the fore (pectoral) fin and pectoral girdle are situated on each side ventrolateral to the pronephric tubules. The pronephric ducts each have a continuous lumen which meet each other just before they open into the cloaca. Mesonephroi are not yet developed. At 13·5 mm. true cartilaginous elements (see De Beer, 1926) and incipient tooth germs are present in the head and pharynx. The pectoral fin rudiments as yet possess no cartilage but chondroblast condensation has taken place (Pl. 1, fig. 1). The left pectoral fin is about 610 μ long, the right 660 μ long. The first sign of cartilage in the pectoral girdle is recognized in the 14 mm. stage, and the length from the front to the girdle to the tip of the fin is about 1·0 mm. on the left side, 880 μ on the right. A well formed alimentary canal is present and incipient mesonephric rudiments are recognizable. Cartilage is developed in the pectoral fins of the 15 mm. larva, which are about 1·2 mm. long. The 16 mm. larva possesses a double opening to the nasal sac leading to the roof of the mouth and a well developed chondrocranium and brachial skeleton. The left pectoral fin is about 2·44 mm. long. the right 2·65 mm. long Just in front of the cloaca in one 16 mm. larva are a pair of small ectodermal thickenings. These pelvic fin blastemata are slightly longer in the second 16 mm. specimen. Pelvic fin rudiments normally appear about six weeks after the pectoral fins (Bridge, 1910).

THE PRONEPHRIC SYSTEM

The pronephros which is situated mesial and dorsal to the the base of the pectoral fin, is extremely urodele-like in appearance. In the 11·5 mm. stage the tubules are somewhat more vacuolated than in older specimens, and the connective tissue which normally surrounds the tubular mass was not developed to any extent in any stage examined. Each pronephros possesses two ciliated

nephrostomial tubules which open into the coelom (Semon, 1901) as in larvae of *Lepidosiren* and *Protopterus* (Kerr, p. 231, 1919) and many urodeles. Situated mesially to the nephrostomes are the paired elongated glomera which arise from the dorsal aorta (Pl. 1, figs. 1, 2.).

During the short range of development studied, in which time the total length of the larva increases by 33 per cent and the mean of the measurements of the nose-to-cloacal length increases by 20·4 per cent various components of the pronephric system significantly change in size. In the 15·3 mm. group the means of the measurements of the nuclear population (47 per cent), total volume of cells (42·5 per cent), overall volume of pronephros (volumes of cells

TABLE 1

Various measurements of the components of the pronephric system, in *Neoceratodus* larvae.

	A	B		C	D
No. of specimens	3	1		4	8
Mean total length of specimens (mm.)	11·5	13·5		15·3 ±0·48	13·6 ±0·69
Mean nose-cloacal length of specimens (mm.)	7·83 ±0·033	8·45		9·43 ±0·475	8·71 ± 0·358
Number of pronephroi	6	2		8	16
Mean ant-post. length of pronephros (mm.)	0·583 ±0·0091	LHS 0·580 RHS 0·600	0·590	0·570 ±0·0119	0·578 ±0·0069
Mean nuclear popn. of pronephros	1567 ±47	LHS 2066 RHS 2036	2051	2302 ±126	1995 ±108
Mean total volume of cells of pronephros (mm.³).	0·0106 ±0·00091	LHS 0·0141 RHS 0·0134	0·0137	0·0151 ±0·00163	0·0132 ±0·00101
Mean total volume of lumen of pronephric tubules (mm.³).	0·0036 ±0·00039	LHS 0·0025 RHS 0·0034	0·0029	0·0045 ±0·00031	0·0040 ±0·00025
Mean overall volume of pronephros (mm.³).	0·0142 ±0·00131	LHS 0·0166 RHS 0·0168	0·0167	0·0196 ±0·00187	0·0172 ±0·00123
Mean internal surface area of tubules (mm.²).	±0·4047 ±0·02278	LHS 0·4128 RHS 0·4751	0·4439	0·5467 ±0·02815	0·4806 ±0·02363
Mean calculated individual cell vol. of pronephros (μ³)	6711 ±479	LHS 6818 RHS 6577	6697	6454 ±495	6581 ±295
Number of glomera	6	2		8	16
Mean ant-post. length of glomus (mm.)	0·550 ±0·0176	LHS 0·560 RHS 0·560	0·560	0·404 ±0·0297	0·478 ±0·0248
Mean total volume of glomus (mm.³).	0·0027 ±0·00026	LHS 0·0026 RHS 0·0024	0·0025	0·0021 ±0·00027	0·0024 ±0·00018
Mean total external surface area of glomus (mm.²).	0·1597 ±0·00910	LHS 0·1663 RHS 0·1677	0·1670	0·1347 ±0·01075	0·1481 ±0·00705
No. of nephrostomes	12	4		16	32
Mean diameter of anterior nephrostome base (mm.)	0·073 ±0·0021	LHS 0·060 RHS 0·080	0·70	0·074 ±0·0033	0·073 ±0·0020
Mean diameter of posterior nephrostome base (mm.)	0·078 ±0·0054	LHS 0·070 RHS 0·060	0·065	0·081 ±0·0077	0·078 ±0·0044
Mean diameter of anterior and posterior nephrostome bases together (mm.)	0·152 ±0·0054	LHS 0·130 RHS 0·140	0·135	0·155 ±0·0087	0·151 ±0·0049

A. 11·5 mm. specimens; B. One 13·5 mm. specimen; the average of the component measurements obtained from both pronephroi is included ; C. Four specimens (mean total length 15·3 ± 0·48 mm.) D. Whole collection of eight specimens of *Neoceratodus* (mean total length 13·6 ± 0·69 mm.).

and lumen together) (38 per cent), internal surface area of the tubules (35 per cent) show a significant superiority over the means of those in the 11·5 mm. group by the stated percentages. The mean antero-posterior length of the glomus is lower by about 27 per cent. Means of the antero-posterior pronephric length, total volume of the tubule lumen, calculated individual cell volume, diameters of the anterior nephrostomial tubule and posterior nephrostomial tubule bases and the diameters of these tubule bases together, total glomus volume and total external surface area of the glomus do not significantly change (Table 1, A & C).

DISCUSSION

Within the range of development studied some pronephric components of *Neoceratodus* grow larger, while others do not significantly change in size. Recent work (unpublished) on pronephric growth in *Rana esculenta* larvae has shown that the pronephric cell volume was about 7000 μ^3 at 12 mm. and had not changed when the mean larval length was about 28 mm. Pronephric cell volume of *Neoceratodus* is equally stable during the period under review. The individual cell volume size range for control and hypertrophied pronephroi of *Triturus cristatus* larvae is between 5500 and 7100 μ^3, or when means are adjusted to the nose-to-cloacal length of 6·33 mm. for the larvae, 6000-6900 μ^3 (Fox, 1956). *Triturus helveticus* specimens with either blocked or unblocked pronephric ducts had a pronephric cell volume size range of 4500-6150 μ^3 (Fox, 1957), and for those specimens which developed in different osmotic media, 3400-7100 μ^3 (Fox, 1959). The individual pronephric cell volume of *Neoceratodus* larvae which is found to lie between about 6500 and 6800 μ^3, is of a similar order to that found in the Amphibia. The structure and development of the *Neoceratodus* pronephric system are extremely similar to those in Amphibia, especially the urodeles (Semon, 1901). Furthermore the position, structure, time of origin and subsequent development of the mesonephros and its relationship to the pronephros and its duct are generally similar in both groups. It is extremely unlikely that these quantitative and qualitative similarities were developed independently in Dipnoi and Amphibia. These organs are certainly homologous and derive from a common crossopterygian ancestry. It is more likely that these crossopterygian ancestors (Romer, 1946) transmitted an already separated 'pronephric-mesonephric' organisation to both groups. If this were the case then the hypothetical archinephros (Goodrich, p. 660, 1930) would be differentiated into separate pronephros and mesonephros elements throughout the ontogeny of the crossopterygian ancestors, and a functional undifferentiated archinephros in vertebrates would thus precede them among some earlier forms.

ACKNOWLEDGMENTS

The preserved material of *Neoceratodus* was obtained from the Department of Embryology, University College London, where it forms part of the collection of the late Professor J. P. Hill. I am grateful to Professor M. Abercrombie for the opportunity to use this material. Acknowledgments are also due to Professor P. B. Medawar for his kind interest, to Mrs R. Marchant and Mr A. Veenstra.

Photomicrographs of horizontal and transverse sections at 10 microns of a 13.5 mm. larva of *Neoceratodus*.

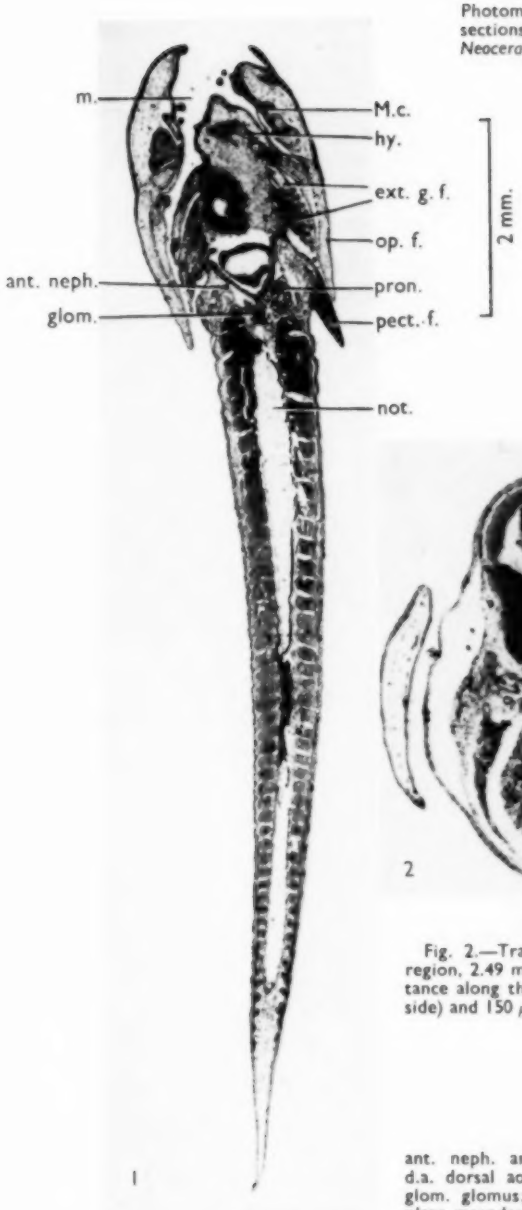


Fig. 1. — Horizontal section through the pronephros and glomus region.

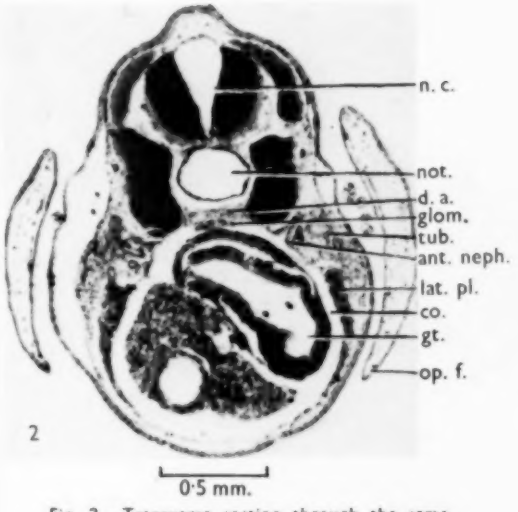


Fig. 2.—Transverse section through the same region, 2.49 mm. from the tip of the snout. Distance along the pronephros is 100 microns (right side) and 150 μ (left side).

ant. neph. anterior nephrostome; co. coelom; d.a. dorsal aorta; ext.g.f. external gill filament; glom. glomus; gt. gut; hy. hyoid; lat.pl. lateral plate mesoderm; m. mouth cavity; M.c. Meckel's cartilage; n.c. nerve cord; not. notochord; op.f. opercular fold; pect.f. pectoral fin; pron. pronephros; tub. pronephric tubule.

REFERENCES

ABERCROMBIE, M. (1946). Estimation of nuclear population from microscope sections. *Anat. Rec.* **94** : 239-247.

BRIDGE, T. W. (1910). Fishes. In *The Cambridge Natural History*. **7** London : Macmillan.

DE BEER, G. R. (1926). The orbito-temporal region of the skull. *Quart. J. Micr. Sci.* **70** : 263-370.

DE BEER, G. R. (1937). *The development of the vertebrate skull*. Oxford : University Press.

EDGEWORTH, F. H. (1935). *The cranial muscles of vertebrates*. Cambridge : University Press.

FOX, H. (1955). The effect of sodium sulphadiazine on the nuclear population of the pronephros in *Tritus cristatus kerelinii* (Strauch). *Exp. Cell Res.* **8** : 250-251.

FOX, H. (1956). Compensation in the remaining pronephros of *Triturus* after unilateral pronephrectomy. *J. Embryol. exp. Morph.* **4** : 139-151.

FOX, H. (1957). The effect of unilateral blockage of a pronephric duct upon the development of the pronephroi in *Triturus helveticus*. *J. Embryol. exp. Morph.* **5** : 274-282.

FOX, H. (1959). A study of environmental influences on the size of the pronephros and related structures in *Triturus helveticus*. *J. Embryol. exp. Morph.* **7** : 257-263.

GOODRICH, E. S. (1930). *Studies on the structure and development of vertebrates*. London : Macmillan.

GREIL, A. (1908 and 1913). Entwickelungsgeschichte des Kopfes und des Blutgefässsystemes von *Ceratodus forsteri*. In Zoologische Forschungsreisen in Australien und dem Malayischen Archipel. *Denkschr. med. naturw. Ges. Jena.* **4** : 661-934, 935-1554.

KERR, J. G. (1919). *Textbook of embryology*. London : Macmillan.

ROMER, A. S. (1946). *Vertebrate palaeontology*. Chigaco : University of Chicago Press.

SEMON, R. (1901). Zur Entwicklungsgeschichte der Urogenitalsystems der Dipnoer. *Zool. Anz.* **24** : 131-135.

SEMON, R. *et al.* (1893-1913). In *Ceratodus* Zoologische Forschungsreisen in Australien und dem Malayischen Archipel. *Denkschr. med. naturw. Ges. Jena* **4** : 1-660.

NOTICE

" Proceedings " Vol. 134, Part 3, was published on 29th July, 1960.

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C.4.

SYMPOSIA OF THE ZOOLOGICAL SOCIETY OF LONDON

This new series has been established to contain the papers delivered at the Symposia held by the Society. The object of the Symposia is to bring together workers who are engaged in research on different aspects of any branch of zoology. The organizer of each Symposium selects the contributors and acts as editor of the published number in which the proceedings are recorded.

No. 1 HORMONES IN FISH. Proceedings of the Symposium held on 13th October, 1959. Edited on behalf of The Zoological Society of London by I. CHESTER JONES. Price £2 0. 0.

No. 2 CYCLICAL ACTIVITY IN ENDOCRINE SYSTEMS. Proceedings of the Symposium held on 8th December, 1959. Edited on behalf of the Zoological Society of London by E. J. W. BARRINGTON. Price £1 5*s*. 0*d*.

Forthcoming issues :—

No. 3 SENSORY SPECIALIZATION IN RESPONSE TO ENVIRONMENTAL DEMANDS. Proceedings of the Symposium held on 4th March, 1960. Edited on behalf of The Zoological Society of London by O. E. LOWENSTEIN. In press.

No. 4 TUBERCULOSIS IN ANIMALS. Proceedings of the Symposium held on 24th May 1960. Edited on behalf of The Zoological Society of London by J. N. RITCHIE.

INSTRUCTIONS TO AUTHORS

Papers submitted for publication are understood to be original works and are to be offered to the Zoological Society of London alone, unless the contrary is stated. They should be addressed to the Scientific Director, The Zoological Society of London, Regent's Park, London, N.W.1, and should be prepared in accordance with the Society's instructions to authors, a copy of which may be obtained from the Librarian and Clerk of Publications on application. The copyright becomes the property of the Society when a paper is accepted.

NOTICE

" Proceedings " Vol. 134. Part 3. was published on 29th July, 1960.

Printed by Taylor & Francis, Ltd., Red Lion Court, Fleet Street, London, E.C.4.

SYMPOSIA OF THE ZOOLOGICAL SOCIETY OF LONDON

This new series has been established to contain the papers delivered at the Symposia held by the Society. The object of the Symposia is to bring together workers who are engaged in research on different aspects of any branch of zoology. The organizer of each Symposium selects the contributors and acts as editor of the published number in which the proceedings are recorded.

No. 1 HORMONES IN FISH. Proceedings of the Symposium held on 13th October, 1959. Edited on behalf of The Zoological Society of London by I. CHESTER JONES. Price £2 0. 0.

No. 2 CYCLICAL ACTIVITY IN ENDOCRINE SYSTEMS. Proceedings of the Symposium held on 8th December, 1959. Edited on behalf of the Zoological Society of London by E. J. W. BARRINGTON. Price £1 5*s*. 0*d*.

Forthcoming issues :—

No. 3 SENSORY SPECIALIZATION IN RESPONSE TO ENVIRONMENTAL DEMANDS. Proceedings of the Symposium held on 4th March, 1960. Edited on behalf of The Zoological Society of London by O. E. LOWENSTEIN. In press.

No. 4 TUBERCULOSIS IN ANIMALS. Proceedings of the Symposium held on 24th May 1960. Edited on behalf of The Zoological Society of London by J. N. RITCHIE.

INSTRUCTIONS TO AUTHORS

Papers submitted for publication are understood to be original works and are to be offered to the Zoological Society of London alone, unless the contrary is stated. They should be addressed to the Scientific Director, The Zoological Society of London, Regent's Park, London, N.W.1, and should be prepared in accordance with the Society's instructions to authors, a copy of which may be obtained from the Librarian and Clerk of Publications on application. The copyright becomes the property of the Society when a paper is accepted.

LIST OF CONTENTS

Vol. 134

Part 4 (pp. 509–663)

Page

Barnett, S. A.
Social behaviour among tame rats and among wild-white hybrids. (1 figure) 611

Burdon-Jones, C. and Patil, A. M.
A revision of the genus *Saccoglossus* (Enteropneusta) in British waters. (3 figures)..... 635

Duncan, C. J.
The evolution of the pulmonate genital system. (1 figure) 601

Fox, H.
Early pronephric growth in *Neoceratodus* larvae. (1 plate) 659

Höhn, E. O.
Seasonal changes in the mallard's penis and their hormonal control. (1 figure)..... 547

Jones, C. Burdon-. See Burdon-Jones, C.

Krohn, P. L.
The duration of pregnancy in Rhesus monkeys *Macaca mulatta* 595

Murphy, D. H.
Collembola Symphypleona from the Gambia, with a note on the biogeography of some characteristic savanna forms (132 figures)..... 557

Napier, J. R.
Studies of the hands of living primates (3 plates and 3 figures).... 647

Paterson, Nellie F.
The inner ear of some members of the Pipidae (Amphibia). (14 figures) 509

Patil, A. M. See Burdon-Jones, C.

Willmott, Sheila.
The morphology of *Brumptia bicaudata* (Poirier, 1908) Odhner, 1926 (Trematoda : Paramphistomoidea). (9 figures)..... 623

Title Page, List of Contents and Index.

NOTICE

" Proceedings " Vol. 134 Part 3 was published on 29th July 1960